The Relation of Desert Plants to Soil Moisture and to Evaporation

BY

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THE RELATION OF DESERT PLANTS TO SOIL MOISTURE AND TO EVAPORATION.

INTRODUCTION.

Every observer of desert vegetation has had his attention drawn to the question of how certain plants of the arid regions are able to maintain a more or less active transpiration during long periods of absolute lack of precipitation, when the soil in which they are rooted becomes not only apparently air-dry but also attains exceedingly high temperatures. It seemed that careful quantitative studies of the moisture conditions in desert soil and desert atmosphere, and of the relation of these conditions to the transpiration and life of desert plants, might throw considerable light not only upon this problem of extreme xerophytism, but also upon the limitations of plant life in general. Just as the alpine summits of high mountains in all parts of the earth and the frozen tundras of the arctic regions exhibit vegetable life under temperature conditions which almost render it impossible, so the arid desert with its centimeters of annual rainfall and its meters of annual evaporation exhibits plant life under conditions of extreme dryness which similarly approach a limit to the very existence of such life. It is thus plausible to suppose that certain fundamental truths regarding the vital activities of plants may be more advantageously studied in the case of organisms existing under these extreme conditions than by confining attention to what are considered the more normal circumstances of life and growth.

With the aid of a grant from the Carnegie Institution of Washington the writer was able to spend the summer of 1904 at the Desert Botanical Laboratory of that Institution at Tucson, Arizona, in carrying out a series of quantitative studies on desert plants. The results of these studies are embodied in the present paper.

Thanks are due to Prof. Frederic V. Coville and Dr. D. T. MacDougal, who constituted the Advisory Committee of the Laboratory when this work was done, as well as to Dr. W. A. Cannon, resident investigator, for the excellent facilities provided at the Laboratory, without which the work could not have been carried out. Mrs. Grace Johnson Livingston has rendered very valuable assistance in the preparation of this paper, especially in the tabulating of the data and in the construction of the curves.

The problems here dealt with concern the relations between certain desert plants on the one hand and their physical environment, consisting of soil and atmosphere, on the other. The importance of animal life as an environmental factor in the desert is undoubtedly very great, but no careful studies were made along this line. The results of the investigations can be best presented under the three headings, "Soil studies," "Atmosphere studies," and "Plant studies," these to be followed by a discussion of the interrelations existing between the facts brought out by the three lines of inquiry.

It was more expedient and seemed altogether more desirable to make a rather thorough study of the conditions obtaining on the shoulder of Tumamoc Hill, in the immediate vicinity of the Desert Laboratory, than to attempt broader and therefore less thorough studies embracing other localities, such as the mesa below the hill and the erosion channels and washes of the Santa Cruz River, Rillito Creek, etc., or of the more distant and more varied Santa Catalina Mountains. A remarkable uniformity in soils and vegetational characters is exhibited by all the peaks and buttes of the Tucson Range, and Tumamoc Hill may be taken as a type of these. Thus the results of the present investigations may be regarded as applicable to the whole range. All these peaks are distinctly desert mountains, not attaining a sufficient altitude to have moisture conditions which will allow any form of plant growth less xerophytic than the *Parkinsonia-Cereus* society which covers Tumamoc Hill. This society comprises, besides the giant cactus or saguaro (*Cereus giganteus*) and palo verde (*Parkinsonia microphylla*), a number of *Opuntia* species, both of the arborescent and prickly-pear types, the barrel cactus (*Echinocactus Wislizeni*), ocotillo (*Fouquieria splendens*), cat's claw (*Acacia greggii*), and occasional creosote bushes (*Covillea tridentata*), together with several other shrubs and numerous smaller plants. This vegetation has been briefly described by Coville and MacDougal (1903) and also by Lloyd (1905).

The Santa Catalina Range, which rises on the opposite side of the mesa, is more extensive than the Tucson Range and much higher. The foot-hills and rugged slopes toward the mesa are very similar in soils and vegetation to the Tucson Mountains, but as the ascent is made new conditions are encountered, largely those of increased moisture and lower temperature, and in the higher altitudes of the Catalinas are streams of running water and forests of oak and needle-leaved trees. The series of vegetational transitions from the willow and ash margined Rillito Creek, across the great sandy washes, where the latter widens in time of flood, on which dwarfed mesquite (*Prosopis velutina*) forms practically the whole vegetational cover in the dry season; across the

level mesa with its creosote bushes (*Covillea tridentata*) and several arborescent species of *Opuntia;* up into the lower slopes of the mountains, sparsely covered, like the Tumamoc Hill, with giant cacti, palo verde, cat's claw, and both arborescent and prickly-pear forms of *Opuntia;* still up into the intermediate region of scattered oaks, agaves, and yuccas, with the beginnings of a real undergrowth of smaller plants; and finally into the true forests of the high mountains—this series of transitions would form as instructive a subject for ecological inquiry as can be afforded anywhere. It was with a distinct feeling of regret that the author returned from a reconnaissance trip through the area of these transitions to take up the more definite problems on Tumamoc Hill.

SOIL STUDIES.

GENERAL CHARACTER OF THE SOIL.

The shoulder of the hill on which the Desert Laboratory is situated rises to an elevation of about 90 meters above the level of the broad mesa below. The mesa surrounds it on all sides, excepting at the south, where the shoulder connects with the flat-topped mountain itself, which attains an elevation of about 200 meters above the plain. The Laboratory building is thus located about midway between the base and the top.

The mountain is composed mainly of volcanic rock broken into fragments on the surface and darkened by weather to a deep brown or black. On the slopes the pockets and crevices between these rock fragments are filled near the surface with a heavy brown clay soil. On the gently sloping and practically flat portion of the shoulder just above the building this soil makes up most of the surface, the superficial rock fragments being here not so numerous nor so large as on the slopes. Even in those places which have the deepest soil, however, the pickaxe and spade very soon reach either the bed-rock of the mountain or masses of rock too large to be readily removed or excavated around. Thus deep diggings are almost, if not entirely, impossible without penetrating the rock itself.

On the mesa below the hill the surface soil is much more sandy and gravelly and few large fragments of volcanic rock are found near the surface. But this soil is underlaid at a depth of a meter more or less by a curious hard-pan of soft and more or less fragmented limestone called "caliche." This is not so hard but that it can be excavated with a pickaxe and is quite permeable to water, although it certainly hinders the downward flow of the latter to a considerable extent.

The caliche layer is perhaps an incrustation brought about by evaporation beneath the soil surface. In the dry season the soil becomes air-dry to a considerable depth, and in this condition water must diffuse as vapor through the interstices of the soil more rapidly than liquid water can move from the moister layers below to the drier ones above. The result is that the evaporating surface of the soil is often, and for long periods, far below the soil surface, and, from this subterranean evaporating surface, water vapor diffuses upward through the dry soil-layers to the air. As is well known, the soil of these regions contains a large quantity of soluble salts. This soil solution, being lifted by evaporation, becomes concentrated, and finally the salts should crystallize out at or near the evaporating surface. In this way the caliche hard-pan may have been formed. Another hypothesis to explain the existence of this hard-pan supposes the caliche to have been formed at the lower limit of penetration for precipitation water, the salts having been gradually deposited as the soil was alternately wet and dry. To definitely determine which of these hypotheses is more probable will require further investigation.

Just as the caliche underlies practically the whole surface of the desert mesa, so too the crevices and fissures on Tumamoc Hill are largely closed by a similar formation at the depth of a meter or less. Plant roots penetrate into the cracks of this hard-pan both on the hill and on the mesa, and it is probably a very important factor in conserving the meager water supply.

WATER CONTENT OF THE SOIL IN THE DRY SEASON.

At the time of the beginning of the work, July 1, 1905, the desert conditions on the hill were nearing their maximum for the year. The surface soil about the Laboratory building was air-dry and seemed thoroughly baked. Day and night air temperatures varied from 80° to 105° F. or above, and the relative humidity of the day time varied between 8 per cent and 15 per cent of saturation. Rain had not fallen since May 12, at which time 1.97 cm. fell, and strong breezes or even gales were almost constant. The only plants which remained in good condition were those which are particularly adapted in some manner to dry habitats. The giant cacti had just finished flowering and were ripening their pulpy fruits, much sought after by Mexicans and Papagos and even by groups of American children who now and then came out from Tucson. Prickly pears were also ripening their fruits, while barrel cacti and several arborescent opuntias showed no marked growth and of course bore no leaves. The creosote bush was green but not growing, and was covered with ripe fruits; many plants of ocotillo had

lost their leaves and stood as groups of gray, spiny wands; many others were still green and appeared healthy, but practically all had scattered their seeds. A single belated cluster of ocotillo flowers was found near the top of the mountain on July 7. The trees of palo verde (*Parkinsonia microphylla*) near the Laboratory had very largely lost their leaves, thus also showing the effect of drought. Of the smaller plants, *Encelia farinosa* still held its own as far as foliage was concerned, and a small red mallow, *Sphaeralcea pedata*, together with a prostrate *Euphorbia*, probaby *E. capitellata* Eng., of somewhat the aspect of *E. polygonifolia* of the East, were producing flowers and seemed perfectly vigorous.

The extreme dryness exhibited by soil, air, and vegetation, together with the fact that the summer season of rains was rapidly approaching, made it seem very important to take up immediately the question of the actual amount of water contained by the soil at that time. Accordingly a great number of diggings were made on the slopes of the hill and on its top around the Laboratory, care being taken not to locate any of these within possible reach either of the water tank, where small amounts of water were usually escaping, or of the outlet of the waste pipe below the building. Samples of soil were collected in this manner from various depths and immediately placed in glass vials, which were tightly stoppered and weighed. The samples were then emptied into Stender dishes, of the form used for staining microscopic preparations, and, in default of a suitable drying oven, left open in the laboratory 5 to 15 days, being stirred occasionally to hasten evaporation. When these had ceased to lose water they were returned to stoppered vials and their weight was again recorded. After the author's return to the University of Chicago these samples were again weighed, dried thoroughly in an oven at a temperature of from 105° to 110° C., and the amount of water thus lost was added to that which had been lost in air-drying at the Desert Laboratory. The amount of water present in the original samples was computed on the basis of volume per cent. While for comparisons between different samples of the same soil the water content may be determined in percentage of the dry weight of the soil, this method fails to have even a practical value when soils of different specific gravities are dealt with. This point, while it has been mentioned by Whitney and Hosmer (1897, p. 7) and others, has never been adequately emphasized from the standpoint of plant physiology. From this standpoint the interesting questions are, first, how much water is within reach of the plant, and, second, how much of this water can be absorbed by the roots? In the answer to the first question the specific gravity of the soil can play but a minor part, the main factor being the volume of soil drawn upon by the roots and

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the actual amount of water contained in this volume. The answer to the second question depends upon the degree to which the soil holds its water as related to the amount of absorptive power exerted by the plant. Thus the availability for any species of any given volume percentage of water in non-alkali soils is determined largely by the fineness of the soil particles and by the physiological properties of the roots. It is only a coincidence that extremely light soils, being mainly organic in their nature, have a comparatively high power to withhold water from plants growing therein.

In order to secure uniformity in compactness the wet volume of the samples was used for this purpose. To obtain the wet volume, a sufficiently large graduate was partially filled with water and the soil poured in and thoroughly stirred to allow inclosed air to escape. The thin paste thus formed was allowed to stand until settling was complete, when the volume of the saturated soil was read directly on the graduate scale. It was found that the amount of soil which would occupy, on settling in water, a volume of 100 cc., weighed, in its oven-dry state, 85.0 grams. The same amount of soil, when merely poured into a graduate without tamping, occupied a volume of 78.9 cc., and when thoroughly tamped as it was poured in it occupied 68.4 cc. Thus the percentage figures of moisture content obtained on the basis of volume when allowed to settle in water are considerably lower than would have been the case had they been computed on the dry volume when either poured into the graduate or tamped. Since uniformity in tamping is very difficult to obtain, the method of tamping could not well be used. The dry surface layers of Tumamoc Hill usually crumble and compress beneath the foot, indicating that the soil of these layers, as it dries out after being wet, occupies a greater volume than it would if it were pulverized. Therefore it seemed that the natural volume would be more nearly approximated by the method here used than by any other, and at the same time a uniform treatment of the different samples could be secured. From the data given above it is clear that the moisture contents here given would have been $\frac{15}{85}$, or 17.6 per cent larger had they been computed on dry weight, as is usually done in such measurements.

By the method just described it was found that the soil samples air dried in the laboratory contained from 2 to 3 per cent of moisture. Samples of the upper 2 or 3 cm. of the natural soil, taken in the burning sunshine between July 1 and July 14, contained somewhat less water, about 2 per cent. In most places on the hill it was impossible, on account of rock fragments or caliche, to make small excavations to a depth greater than 10 or 12 cm. Samples at this depth, lying against

the rock, exhibited a total moisture content of 5 to 10 per cent of their wet volume. A single sample taken at a depth of 15 cm. contained 13.04 per cent of water, and other samples ranged in moisture content from 7 to 12 per cent. It is thus seen that there is considerable variation in contained moisture at the same depth in different places, largely due, no doubt, to the relation of the soil to the surrounding rock fragments and underlying bed-rock or caliche. One digging was made to a depth of 35 cm. and a sample taken from the soil at this depth, lying against solid caliche, which apparently completely closed the opening between the large fragments of volcanic rock which had been followed in the digging, contained 15.16 per cent of water.

It was intended to make larger excavations and determine moisture conditions at greater depth, but the beginning, on July 15, of the period of heavy rains made this seem of no avail. The structure of the surface layers of the hill, composed, as it is, of mingled rock fragments, offers many chances for water from the surface to find its way to the lower levels along rock surfaces, especially as all the superficial hollows and rock pockets stand full of water for some time after each heavy shower. The soil puddles and becomes itself very slowly permeable to water, but the latter was shown, by diggings made shortly after the first rain, to have attained the depth of the larger rock masses by following down the surfaces of rocks which were exposed above.

From the moisture determinations which were made it is evident that this soil does contain, during the driest season of the year, rather large amounts of water, and this at no great depth. Spalding (1904) found, about April 24, 1904, that a sample of soil of this same locality, at a depth of 30 cm., contained 8 per cent of its air-dry weight of water. The same author says, "Another sample from the hill [presumably at the same depth] lost, by heating over an electric stove, 12 per cent of its weight." From the relations of weight and volume given above it is easy to reduce this result to the approximate percentage by volume under water. As above stated, the per cent of water content calculated on the dry weight of the soil is 17.6 per cent greater than that calculated on wet volume. Thus Spalding's 12 per cent is 1.176 times the corresponding water content figured by the method here used, and we have the condition: $1.176v=12$, wherein v is the percentage of contained water on the basis of wet volume. From this it appears that $v=10.2$ per cent.

It is probable that the method of drying over the electric stove failed to remove all the water from the soil sample, and this may partially account for the fact that the figure just derived is somewhat lower than would be expected from the determinations given

above. As has been noted, however, conditions other than depth seem to play a part in determining the moisture content on this rocky hill, great variations being manifested in a number of samples taken from different places at the same depth.

The surprisingly large amount of water contained in this soil relatively quite near its surface is probably very largely due, paradoxical as it does indeed seem, to the excessively high rate of surface evaporation. After a number of heavy showers, when the soil is quite moist to an indefinite depth, the first few centimeters lose water much more rapidly by evaporation into the air than it can be supplied by the much slower process of diffusion upward through the soil films from lower-lying layers. The result is that there is soon formed a very perfect mulch of air-dry soil, similar to the "dust mulch" of the agriculturists. In this condition the rate of water loss from the true evaporating surface, which now lies at some depth within the soil, is governed, not by the power of the free air to vaporize water, but by the rate of diffusion of water vapor through the nearly air-dry layers which lie above. This subject will be again considered in the chapter devoted to atmosphere studies.

In the chapter devoted to plant studies the question of how much water is needed in the soil in order that seeds of desert plants may germinate and develop into seedlings will be considered, and experimental evidence will be brought forward pointing clearly to the conviction already noted by Spalding (loc. cit.) that sufficient moisture is probably at all times present in the deeper layers of these soils for the needs of transpiration and even growth of the desert plants which root deeply enough to reach those layers. That there is considerable variation in the water content of the deeper soil layers of Tumamoc Hill is shown by the fact already stated, that at the end of the spring dry season *Fouquieria* plants which had not lost their leaves were numerous, while many others were leafless, the latter apparently indicating a paucity of water in the soil within reach of their roots. It is possible that the latter plants were so situated that their roots did not reach moist soil on account of solid rock or large rock fragments.

PERMEABILITY OF THE SOIL TO WATER AND RATE OF DOWNWARD MOVEMENT.

As has been stated, the season of summer rains began on July 15. From this date until September 1 heavy showers were frequent, sometimes several on the same day, sometimes at intervals of several days, and with each shower the surface of Tumamoc Hill was thoroughly flooded with water. The precipitation flowed off from the general sur-

face very rapidly, but always stood in the pockets and hollows for several hours after the cessation of the rain. The surface soil became saturated anew with each shower, but usually dried out quite thoroughly before the next. The downward penetration of the water into the lower soil layers continued, however, between the showers, and by August 1 the soil had become quite moist to the depth of 20 or 30 cm. This downward movement of water is hindered, as has been stated, by the puddling of the soil, but is hastened by the presence everywhere of oblique rock surfaces down which water movement is much more rapid than it is through the soil itself. It is thus seen that during the rainy season the deeper layers of soil receive considerable quantities of water by direct downward movement from the surface. It is also probable that greater or smaller amounts of water find their way through the soil of the upper part of the mountain to the underlying rock and thence flow down the slope beneath the soil surface and penetrate into all the crevices, whether or not these are closed by caliche, the latter being always quite readily permeable. Altogether, it is highly probable that, for periods of many days during the latter part of the summer rainy season, the entire soil of the mountain, with the exception of the first few centimeters, is very moist and offers abundant opportunity for growth of roots. The most superficial layers themselves are often very moist for periods of several days at a time, when showers follow one another at frequent intervals. Thus seeds might germinate at or near the surface, when the soil contains sufficient moisture, and the seedlings might, by the rapid downward development of roots, easily attain, before the end of the rainy season, to depths where the water content is permanently as great as 10 or 12 per cent.

Measurements of the rate of downward movement of water in the soil when air-dry were made by several experiments. Six cylindrical tumblers 5 cm. in diameter and 11 cm. high were filled to a depth of of about 9 cm. with air-dry soil moderately tamped, water was poured upon the surface of each so as to stand about 1 cm. above the soil, and measurements of its rate of downward penetration were made from minute to minute for a period of 15 minutes. The water above the soil was kept at a nearly constant level by adding more as it disappeared. The average rate per minute for the several intervals was determined for the six soil columns. During the first minute the water penetrated 3.1 cm., during the second 0.8 cm., during the third 0.5 cm., during the fourth, 0.5 cm., and the rate of advance gradually diminished until at the end of 15 minutes it had fallen to 0.2 cm. per minute, the decrease being now exceedingly slow. During the entire period of 15 minutes the water had penetrated, according to these averages, to a depth of 7.5 cm.

It seemed possible that the rate of movement here found was too high for the natural soil on account of the fact that the latter is apt to be more firmly packed than was the soil in these columns. Therefore a similar tumbler of soil was prepared, tamped as firmly as possible, and the rate of water penetration into it studied in the same way. The upper surface of the column was not packed as firmly as the soil below, and the initial rate of advance of the water was nearly as rapid as that in the previous experiment. In two minutes it had advanced 2.5 cm., during the third minute its increment was 0.2, during the fourth it was the same, during the fifth it was 0.15, and this rate decreased so that at the end of 3 hours the soil was moist to a depth of only 4.8 cm. below the surface. It thus appears that the rate observed in the case of the first set of six tumblers is perhaps about twice as great as in the natural soil. It was deemed worth while, however, to study the decrease in the rate of penetration in the case of a longer soil column only moderately tamped. This column was 4.5 cm. in diameter and 93 cm. high, a column of water being kept about 2 cm. high above the soil. The experiment was continued for 30 hours, observations being taken from time to time and the hourly rates of water movement being calculated from the observed increments. These rates, in centimeters per hour, are expressed in the form of a curve in figure 1 (p. 15). In this curve abscissas denote time, the numbers on the horizontal axis representing hours. The ordinates denote the rates and are plotted at the middle of the time periods to which they correspond. These rates are placed adjacent to the points marked by crosses, which determine the position of the curve. It will be observed that, after the first five hours, the rate of downward movement decreased quite uniformly to the end of the experiment. During the last three hours the rate was about 1.3 cm. per hour, the record ending when the water had reached a depth of 42.4 cm. below the soil surface.

Data on the question as to the exact relation of these figures to the natural conditions near the Desert Laboratory during the summer rains were not obtained, but the fact was established that, as early as August 1, the moisture of precipitation had penetrated to a depth of from 20 to 30 cm., thus connecting, by means of moist soil, the surface layers with the lower-lying ones, which were moist at the beginning of the rains.

RETAINING POWER OF THE SOIL FOR PERCOLATING WATER.

The power of soils to absorb and retain water and prevent its downward flow into lower layers varies exceedingly according to their nature. The coarser the soil particles and the smaller the amount of organic débris contained, the smaller will be its retaining power. Thus, in
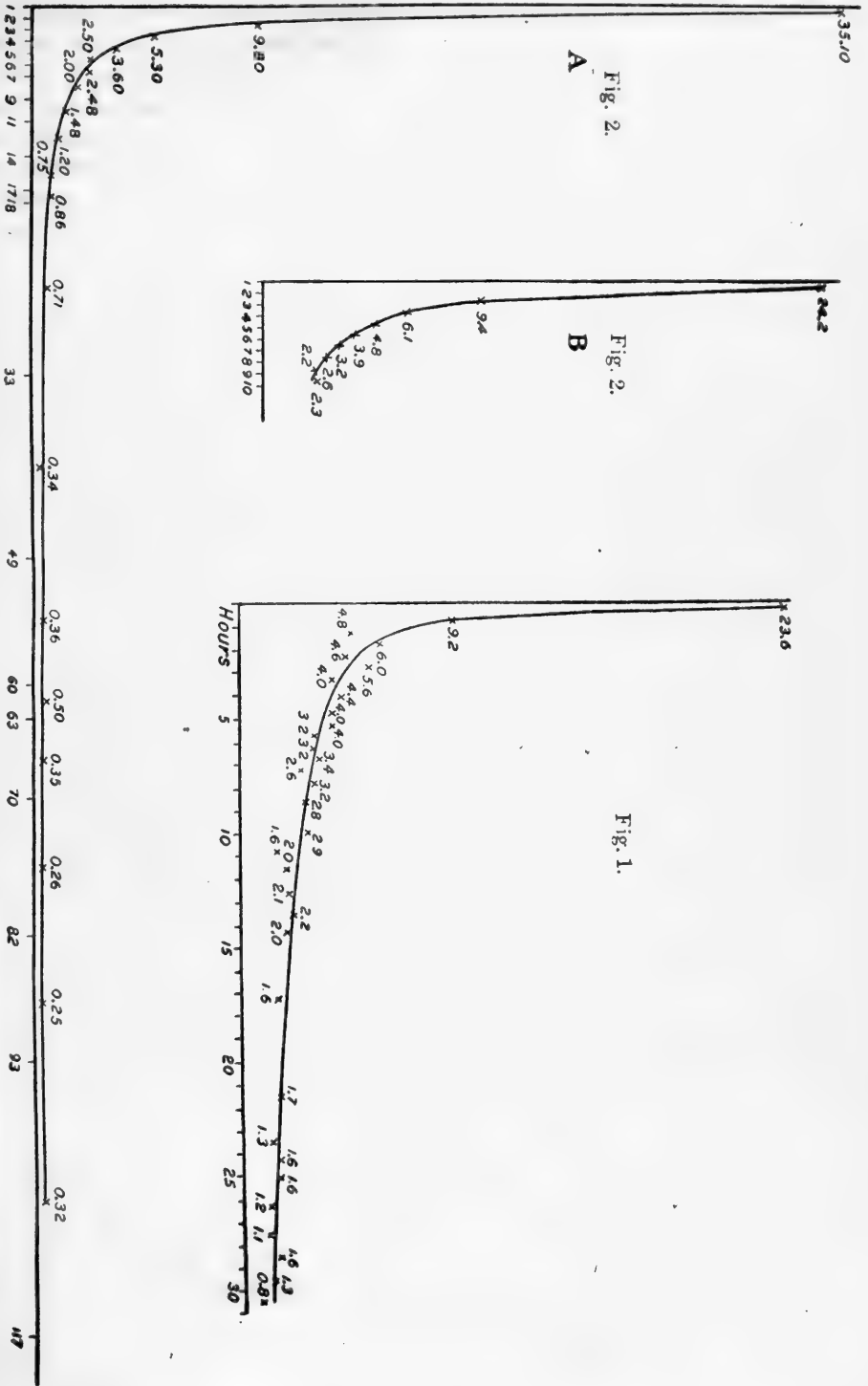
Fig. 2.

Fig. 2.

A

B

Hours

Fig. 1.

FIG. 1.—Curve of rate of downward movement of water in air-dry soil.   FIG. 2, A and B.—Curves of rate of rise of water in air-dry soil.

the case of sandy soils lying above the level of underground water, the water of a heavy shower percolates rapidly and is drained away below, leaving but a small amount in the upper layers. But in clay soils a very much larger amount of water is held by capillarity and fails to drain away. For this reason, in regions where long periods elapse between rains, those upland soils which are more clayey in their nature are uniformly better adapted to plant growth during the periods of drought than are the more sandy ones which retain less water. For a discussion of this subject in reference to more humid regions the reader is referred to publications by Warming (1902, p. 55), Schimper (1898, p. 94), Livingston (1905), and Livingston and Jensen (1904).

As should be expected from its nature, the clay of Tumamoc Hill has a high water capacity or retaining power. Determination of this property was made by the usual method. A tin cylinder, 13 cm. high and 8 cm. in diameter, with a perforated tin bottom covered externally with cloth, was used for this purpose. This vessel was partially filled with soil, tamped in, and the whole was weighed. Then the cylinder was placed upright in water, so that the surface of the latter was somewhat above that of the soil within, and water was poured in above the soil until it stood several centimeters deep above the latter. When the soil was thoroughly saturated the cylinder was removed and allowed to drain until water ceased to flow out through its bottom, after which a second weighing was made. Finally, the volume of the soil when allowed to settle under water was determined, and the difference between the two weights taken as the amount of water retained by the soil. This was calculated in percentage of the wet volume of soil used, of the dry volume tamped, and of the dry volume not tamped. An average of five such determinations gave the amount of water retained by this soil as 40.9 per cent of its wet volume, 59.8 per cent of its dry volume tamped into the cylinder, or 51.8 per cent of its dry volume not tamped. This water capacity, or retaining power, is very high, although it does not reach that possessed by some of the heavy clays of Michigan which the author has dealt with. One sample from that State had a retaining power of 62.5 per cent of its dry volume untamped.

From the determination just given it is evident that the soil under consideration retains, and prevents from draining away below, an enormous amount of water, and to this fact is probably due the prevalence on the hill of a number of plant forms which derive most of their water from near the surface. *Cereus* and *Echinocactus* are examples of these. It is clearly shown by the work of Mrs. E. S. Spalding (1905) on *Cereus* that this plant derives most of its storage water from the surface layers when these have a high moisture content following a

shower. These plants begin to absorb water and to swell almost immediately after the surface soil about their bases is wet either by rain or artificially. The more sandy and gravelly soils of the surface of the mesa at the foot of the hill possess this property of holding water to a much less degree, and water falling upon them readily finds its way to the lower levels and finally to the drainage channels of the Santa Cruz River and its branches. No doubt this sandy character of the mesa soil furnishes the main reason why the vegetation on the mesa here is so much more xerophylous in character than that on Tumamoc Hill. Between the base of the latter and the Santa Cruz sand-wash practically the only plant to be seen in the dry season is the creosote bush, and the specimens of this shrub here found are not by any means so vigorous as those growing in the clay soil of the hill. The same condition of things is to be observed in the relation of the mesa vegetation on the other side of Tucson to the vegetation which occupies the foothills of the Santa Catalina Range.

POWER OF THE SOIL TO RAISE WATER FROM LOWER LEVELS.

The power of a soil to raise water, by capillarity, from the lower-lying layers follows very closely its retaining power. The rate at which this water movement takes place and the height reached by the water above the source of supply depends primarily upon the smallness of the capillary spaces of the soil, and hence upon the fineness of the component particles as well as upon their degree of compactness.

Capillary lifting power is most often measured by filling a vertical glass tube with soil, placing its lower end in water, and measuring the rate at which the water ascends the soil column, this being determined by the change in the color of the soil as it becomes moist. A better, though much slower, method for determining the maximum height to which water will thus rise is to saturate a tube of the soil, place its lower end in water, and determine the maximum depth from the upper surface to which the soil becomes dry. The latter method was attempted with the soil under consideration, but the author's time was too limited to obtain any evidence therefrom.

By the other method results were obtained which warrant presentation here, although the soil columns used were undoubtedly much less thoroughly packed than is the natural soil. The afternoon of August 2, a vertical glass tube of 1.8 cm. internal diameter was filled with air-dry soil, after having its lower end closed by tying a layer of cloth over it. The tube was tapped rapidly on the floor while the soil was slowly poured in, so that the latter was fairly compact when the tube became filled. The lower end of the filled tube was placed in a vessel of water

and the height of the moist column of water was noted from time to time. At 4ʰ20ᵐ p.m. the height of this column had attained to that of the water outside the tube and from this time on the rise of the liquid through the soil was due entirely to the capillary power of the latter. The level of the external water was kept approximately at the same height by addition of water as needed, evaporation from the free water surface being avoided by covering this with oil. After September 3 several readings on this apparatus were very kindly made by Dr. W. A. Cannon.

The results of these determinations are given in Table I. The first column gives the times of observation, the second the observed height of the column of moist soil above the water level outside the tube, and the third gives the average rate per hour of the rise of the liquid during the period just ending.

TABLE I.—*Rise of Water in Air-dry Soil.*

Date and hour.	Height of moist soil above water level.	Rate of ascent per hour.	Date and hour.	Height of moist soil above water level.	Rate of ascent per hour.
	cm.	*cm.*		*cm.*	*cm.*
Aug. 2, 4ʰ 20ᵐ p.m.	o	o	Aug. 8, 8ʰ 50ᵐ a.m.	57.9	0.104
5 11 p.m.	4.8	5.16	Aug. 10, 8 30 a.m.	61.9	.083
6 00 p.m.	7.8	3.96	Aug. 12, 8 00 p.m.	65.6	.061
7 00 p.m.	11.2	3.40	Aug. 15, 6 00 p.m.	69.0	.048
7 40 p.m.	13.2	3.00	Aug. 18, 10 00 a.m.	71.0	.031
9 00 p.m.	16.4	2.40	Aug. 19, 2 30 p.m.	72.0	.035
Aug. 3, 7 00 a.m.	29.2	1.28	Sept. 3, 5 00 p.m.	82.7	.029
12 50 p.m.	33.3	.683	Sept. 19, 7 00 p.m.	88.2	.014
9 00 p.m.	38.0	.587	Sept. 30, 9 00 a.m.	92.2	.015
Aug. 4, 8 30 a.m.	42.5	.391	Oct. 3, 10 00 a.m.	94.2	.027
6 30 p.m.	45.7	.320	Oct. 10, 12 00 m.	96.7	.015
Aug. 5, 9 00 a.m.	48.9	.220	Oct. 22, 11 00 a.m.	99.8	.011
6 30 p.m.	50.6	.179	Nov. 2, 2 00 p.m.	102.6	.010
Aug. 6, 12 30 p.m.	53.2	.144	Nov. 26, 11 00 a.m.	110.2	.013
Aug. 7, 12 00 m.	55.7	.106			

A curve of these results is given at *A*, figure 2 (p. 15). Time increments are plotted on the horizontal axis in days and rates per day in centimeters on the vertical axis. The curve shows graphically the decrease in rate of upward advance of the moist soil column as it rises above the water level.

From these data it is to be observed that during the first three days the water has risen in this soil a distance of 50 cm., and that it had risen a meter in 81 days. At the end of the last-named period its rate of advance was about one-tenth millimeter per hour.

Another experiment, showing similar results, was performed with the same soil after the author's return to Chicago.   This extended over a period of only ten days.   The results are given at *B*, figure 2 (p. 15). It is seen to be the same form of curve as the previous one.

RESISTANCE OFFERED BY THE SOIL TO WATER ABSORPTION BY ROOTS.

There are in general three conditions under which plant roots fail to absorb water from the soil.   First, the soil may not contain an adequate supply; second, the supply may be adequate but the solutes dissolved in the water may not permeate the protoplasm of the root hairs and may be of so great a concentration that plasmolysis occurs; and, third, the soil may contain poisonous substances which injure the roots and make absorption impossible, even though the physical concentration of the soil solutions may not be great.   Although the soils of Tumamoc Hill contain a rather high percentage of soluble salts, it is not probable that the second of the conditions just mentioned is ever effective here to prevent water absorption.   As the soil dries out, however, plants finally wither from lack of moisture, and this may be due to either or both of the other two conditions.

The first condition, lack of adequate water supply, may be effective to check absorption in two ways.   First, the actual water content of the soil may be too low, and, second, there may be sufficient water in the soil to supply the plants in question for many days, and yet the plants may suffer because the rate of movement of this water may not be sufficiently high to supply the soil layers immediately surrounding the roots as fast as these layers are exhausted by absorption.   These two conditions are closely related and difficult to separate.   Also, as water is removed from the soil, the concentration of the soil solution may increase, so that it is somewhat difficult to distinguish, as the critical point is approached, between actual paucity of water and the effects of high osmotic pressure.

No attempt was made to analyze these factors by experiment, but some interesting data were obtained in regard to the tenacity with which this soil holds water against the osmotic pressure of a sugar solution.   Whether or not absorption in roots is primarily a phenomenon of osmosis, we may be sure that the osmotic condition of the root hairs is of fundamental importance in the process.   If the root hairs are plasmolyzed absorption can not proceed normally.   Therefore it is of the utmost importance to study the relations existing between an osmotic cell and soils which contain various amounts of water, and it was along this line of inquiry that experiments were instituted.

The suggestion is due to Whitney and Cameron (1903, p. 54) that we may attack this subject by means of an artificial root hair, in the form of the ordinary osmometer, consisting of a semipermeable membrane precipitated in porous clay and filled with a solution of known osmotic pressure. Following this suggestion a number of porous clay cylinders or cups were obtained for the preparation of osmotic cells. These were designed especially for this work. They are hollow cylinders of unglazed porcelain, 12.5 cm. in length and having an internal diameter of 2 cm. and a thickness of wall of about 3 mm. One end is closed and rounded, the same thickness of wall being retained here as at the sides. The other end is open and grooved within so as to give good surface of contact for a rubber stopper, while the thickness of the wall is doubled here for a distance of 2 cm. back from the edge, the thickened portion terminating in an external shoulder. A working drawing for one of these cells is shown in figure 3.

In preparing the osmometers, the precipitation membrane of copper ferrocyanide devised by Pfeffer (1877) was employed. The cylinders were boiled in distilled water to expel air and allowed to cool under water. They were then filled with n/10 potassium ferrocyanide solution and were placed upright in a beaker containing copper sulphate solution of equivalent strength, the surface of the external solution being just below the upper edge of the porcelain. In this condition the cells were allowed to stand from two to five days, at the end of which time a good semipermeable membrane of copper ferrocyanide was usually found to have been formed within the porous wall. When the membrane was judged to be complete the cells were removed, thoroughly washed with water, and filled with a 1.5 molecular solution of cane sugar. The opening was tightly closed by a rubber stopper with a single perforation, through which passed a glass tube of about 4 mm. bore. The tube extended above the stopper a distance of about 50 cm. In the act

FIG. 3.—Mechanical drawing for porous clay cylinder for use in osmotic experiments and in evaporimeter.

of closing care was taken to include no air and in pressing the stopper into place the column of solution was forced up into the tube to a height of several centimeters. After the cylinders were filled and stoppered they were placed in water for several hours and only those which failed to leak sugar were used in the experiments.

After testing with water the osmometers were placed in soils from the vicinity of the Desert Laboratory, containing various amounts of water, and observations upon the height of the column of solution were made at intervals for a period of from 10 to 24 hours to determine whether water movement took place from the cell into the soil or in the opposite direction. Of course the osmometers act like water thermometers and slight changes in the height of the columns will accompany variations in temperature. A thermometer was placed in the soil and in the critical cases care was taken to have the soil temperature at the time of observation approximately the same as at the start. In these experiments the soil was placed in tin cylinders of the form used in determining its power to hold water, but without perforations in the bottom. The soil was worked up with the required amount of water and was tamped firmly into the cylinder around the osmometer, the upper suface of the soil being on the same level as the top of the rubber stopper.

Five different osmometers, each used several times, gave the following result: In soils containing 5, 10, and 15 per cent of water by volume the column of sugar solution gradually sank, showing that water was being extracted from the cell. In the 20 per cent soil a very slight rise was noted in some tests and an equally slight fall in others; this soil seems to have approximately the same attraction for water as has a 1.5-molecular cane-sugar solution. In the 25 per cent soil the column of sugar solution rose, showing that the cell was absorbing water from the soil.

We may conclude, then, that the force with which the 20 per cent soil resists absorption of water by one of these osmotic cells is about equal to the osmotic pressure of a 1.5-molecular cane-sugar solution, or, according to Morse and Frazer (1902), about 54 atmospheres. This pressure is surprisingly high, much higher than the osmotic pressure of most plant cells, and suggests that either the osmometers here used do not form as good contact with the soil grains as do the root hairs, or else that osmotic pressure does not indeed play the important part in water absorption which has hitherto been assigned to it.

At the University of Chicago, during January and February, 1905, a number of experiments similar to the above were performed upon a very finely divided quartz sand. The sand used .was the finest one of

the experiment of Jensen and the author (1904) upon the relation of size of soil particles to plant growth. This sand has a water capacity of about 46 per cent by dry volume.

In these experiments the osmometers were filled with a solution of cane sugar having a concentration of 2 gram molecules per liter. Rubber stoppers with two perforations were used and a thermometer was inserted in each cell beside the glass tube, so that the temperature of the solution could be recorded with the readings on the height of the column, and corrections could be made for temperature variations.

It was found that the cell failed to absorb water from sands with a water content of 1.5 per cent by volume; that neither absorption nor water loss occurred in a sand of 5 per cent, and that absorption took place from those of 7.5 and 10 per cent. It thus appears that the force by which water is held in the 5 per cent sand is about equal to that of a 2-molecular cane-sugar solution, or at least 72 atmospheres.

While the experiments with this form of "artificial root hair" have not been carried far enough to justify any theoretical interpretation of the results obtained, enough has been done to show that this method offers a very valuable means for quantitative studies of the mechanics of root absorption. It is hoped that further work may be done along this line. A comparison of the results obtained upon the same soil by this means and by means of the artificial root hair of Briggs and McCall (1904) should throw light upon both the tenacity with which moisture is held by a soil and the rate of movement of soil water.

SUPPLY OF WATER TO THE SOIL.

Situated about 80 meters above the Santa Cruz sandwash, Tumamoc Hill must receive all of its natural water from precipitation. The annual precipitation here is practically the same as that at Tucson, for which station records are available. These records, for fifteen years, as given by Coville and MacDougal (1903, pp. 26, 27), show a mean annual precipitation of 30.10 cm. (11.74 inches), which is distributed mainly in two rainy seasons—one in winter and early spring and one in midsummer. This is shown clearly in Tables II and III, the first of which presents mean monthly precipitations and the second the actual record of precipitation at the Laboratory from May 11 to December 31, 1904. The data are for the 24 hours ending 8 a. m. on the date given. For curves of the annual precipitation and average temperature at Tucson, the reader is referred to Cannon (1905). Dr. Cannon has kindly furnished the author with the data for Table III.

During the summer rainy season of 1904 the surface soils of Tumamoc Hill were often wet and almost continually moist. As has been noted, it is probable that during the heavy showers considerable quantities of water penetrate to the deeper soil masses along rock surfaces and a relatively large amount is often held for several days in

TABLE II.—*Mean Monthly Precipitations at Tucson, Arizona.*

Month.	Centimeters.	Inches.	Month	Centimeters.	Inches.
January	2.03	0.79	July	6.15	2.40
February	2.31	.90	August	6.67	2.60
March	1.97	.77	September	2.97	1.16
April	.69	.27	October	1.64	.64
May	.36	.14	November	2.08	.81
June	.67	.26	December	2.56	1.00

TABLE III.—*Precipitation Record from May 9 to December 31, 1904.*

Date.	Rainfall. Centimeters.	Inches.	Date.	Rainfall. Centimeters.	Inches.
May 11	1.21	0.47	August 17	0.077	0.03
May 12	1.97	.77	August 19	1.51	.59
May 15	.10	.04	August 23	.51	.20
June 18	.10	.04	August 25	Trace	......
July 15	.90	.35	September 2	2.49	.97
July 23	.72	.28	September 13	.28	.11
July 25	.038	.015	September 17	1.28	.50
July 26	.038	.015	October 24	.13	.05
July 30	2.38	.93	October 28	.051	.02
July 31	1.21	.48	November 4	.103	.04
August 4	.59	.23	December 5	.28	.11
August 6	.87	.34	December 8	1.38	.54
August 7	.18	.07	December 9	.44	.17
August 14	Trace	.....	December 23	.077	.03
August 16	1.46	.57	December 31	.56	.22

hollows of the soil, so that time is allowed for direct penetration downward. Nevertheless, it must be remembered that, owing to the relatively low permeability of these soils, a large proportion of the water which falls in the heavy rains fails to soak into the puddled surface and finds its way to the mesa below, where it rapidly drained away to the Santa Cruz.

But, from the facts presented in the discussion of the water content of this soil it is clear that what water does attain to the depth of half a meter or more is well protected from soil evaporation and will

not be likely to escape into the air to any great extent, excepting through the transpiration of plants. A discussion of the conservation of moisture by this soil will be given under the succeeding heading.

ATMOSPHERE STUDIES.

GENERAL PROBLEM.

Aside from the ravages of animals, desert conditions in the locality under discussion are brought about mainly by two different, though related, factors—dryness of the soil and excessive evaporating power of the air. The former factor offers resistance to the absorption of water by plant roots, and the latter accelerates water loss by transpiration from the leaves and stems, so that both factors work together to bring about the extreme xerophytism so manifest everywhere in the aspect of the vegetation.

The soil conditions have been discussed in the previous section. There will now be presented the results of some measurements of the evaporating power of the air. This depends upon two conditions—relative humidity and air movements. Temperature variations affect the evaporation rate through changes in relative humidity. Relative humidity acts directly through alterations in the vapor tension of water. As is well known, a wind increases the rate of evaporation very markedly by furnishing a constantly renewed air layer against the evaporating surface and thus preventing, to a greater or less degree, the local rise in relative humidity which would otherwise occur. Both of these factors are of the utmost importance in influencing the transpiration of plants, and the latter deserves more attention than has heretofore been given to it by most plant physiologists. The only important investigations of the effects of air currents upon the transpiration rate are those of Wiesner (1887), who has shown that, while in certain cases wind causes a closing of the stomata, it usually does not have this effect, but causes a marked rise in the rate of water loss. Eberdt (1889) has corroborated these results of Wiesner.

The data obtained in regard to the evaporating power of the air will be given under two headings: "Evaporation from a water surface," and "Evaporation from the soil."

EVAPORATION FROM A WATER SURFACE—A NEW FORM OF EVAPORIMETER.

Measurements of evaporation are usually made by direct determination of water loss (in terms of either volume or weight) from some sort of vessel of water, the upper surface of which is open to the air. Even though comparatively small readings can be taken, this method is not

sensitive to slight variations from hour to hour, due to air currents, etc., for, as soon as the water surface falls below the upper edge of the containing vessel, this surface is protected, to some extent at least, from the full action of the wind. In attempting to relate plant transpiration to physical evaporation it became necessary to devise a form of evaporimeter which should, if possible, be as sensitive both to variations in air currents and to those in relative humidity as the plant itself. At the same time it should be capable of giving readings for short periods of time, so that changes in the rate of evaporation from minute to minute and from hour to hour might be studied.

Happily, a method was hit upon, which, while it gives practically perfect results, is exceedingly easy of operation and requires a minimum of time and care. The apparatus consists essentially of one of the unglazed porcelain cylinders described on page 20, closed by a rubber stopper carrying a glass tube, the opposite end of which is connected with the outlet of a burette. When the cylinder is placed considerably above the level of the top of the burette and the whole apparatus is filled with water, the pressure of the air is entirely removed from the water in the cylinder, since the water films across the capillary pores of this porcelain will support at least one atmosphere of air pressure, and thus the liquid fails to flow down into the burette. At the same time, evaporation of water from the surface of the moist porcelain is constantly accompanied by a corresponding outward seepage from within, and therefore also by a corresponding withdrawal from the burette. Evaporation from the meniscus of the burette column is prevented either by an oil layer, as shown in figure 4, or by a nearly air-tight closure of the top of the burette, using an inverted test tube or a cork stopper with a small opening cut in one side. The last method is most satisfactory. Readings are taken from time to time of the contents of the burette, and the difference between any two readings gives the volume of water lost from the evaporimeter surface for the period of time intervening between these readings. Only distilled water should be used, since the gradual accumulation of salts within and on the walls of the cylinder alters appreciably the rate of evaporation and thereby introduces an error into the record.

For ease in filling the burette its inlet tube was connected with an elevated separatory funnel, so that it could be refilled at will by simply opening the cock at the base of the latter. The whole apparatus may be mounted on a ring-stand so as to be easily portable (see fig. 4), or the evaporimeter tube may be fixed permanently out of doors and the burette and reservoir may stand in a room, the two parts of the instrument being connected by a tube which passes through the wall,

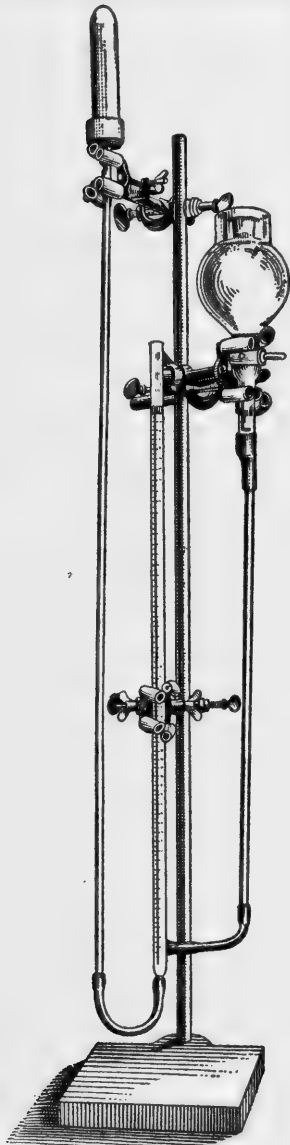For most of the work at the Desert Laboratory the fixed form of evaporimeter was used. The porcelain cylinder was supported vertically, with the stopper uppermost, on a wooden arm reaching out from a window-casing on the north side of the building. The center of the cylinder was 50 cm. from the stone wall of the Laboratory and 2 meters above the ground. It was well under the projecting eaves of the building and was thus protected to a great extent from rain. The sun shone upon it for a few hours in the early morning and again in the late afternoon. The connecting tube, partly of glass and partly of rubber, passed into the building through a hole bored in the window-casing. A burette of 100 cc. capacity was used and stood on a support inside the window, at such height that its upper end was several centimeters below the base of the porcelain cylinder outside. The window was kept closed, excepting when momentarily opened to obtain data for other experiments carried on in the same place, which will be described farther on. An air thermometer, graduated in degrees Fahrenheit, was placed outside the building near the evaporimeter and readings upon it were taken whenever the burette was read.

For absolute measuremements of evaporation it is necessary to calibrate each evaporimeter by exposing for some time and in the same place an open vessel of water with a known area of exposed surface, and weighing this vessel whenever a reading is taken on the evaporimeter. From data thus obtained a coefficient is easily derived by which to multiply any increment of loss from the evaporimeter in order to obtain the rate of evaporation for the same period from any assumed standard area of free water surface. After such calibration has been accomplished, the evaporimeter may be operated indefinitely, care being, of course, taken never to allow air to enter the cylinder. In this work the precaution was taken to wipe off the porce-

FIG. 4.—Evaporimeter, consisting of porous clay cylinder, burette, and water reservoir, the latter in the form of a separatory funnel.

lain evaporating surface from time to time with a moist cloth, to remove dust which was observed to accumulate thereon, especially during the dust storms so frequent in the desert.*

It was thought at the outset that the length of the water column to be lifted by evaporation might influence the rate, so that an error would be introduced by the gradual increase in the height of this column as water was removed from the burette, but this was found by actual tests not to be true. Apparently the tensile strength of the capillary films in the porcelain is so great that their curvature is not appreciably altered by changes of a meter or less in the height of the water column. It was found, however, that if the top of the water column in the burette was above the evaporating cylinder, water was slowly forced out of the latter and appeared as dew upon its surface. Therefore the cylinder was placed, as stated, well above the level of the top of the burette. Had the height of water column appeared to exert any influence upon the rate of evaporation the burette might have been refilled after each reading, but thorough preliminary tests showed this to be unnecessary.

The calibration figures for the fixed evaporimeter above described will now be given. For measuring the loss from a free water surface, a cylindrical glass' crystallizing dish of 118.82 sq. cm. cross section and about 5 cm. high, filled with distilled water, was used. This was suspended by means of wires from a wooden arm similar to the one supporting the evaporimeter cylinder, projecting from the other side of the same window out of which the evaporimeter was placed. The dish was so arranged that its upper surface was at the same height from the ground as the center of the porcelain tube, and also the same distance from the Laboratory wall, thus occupying a position corresponding to that of the evaporimeter cylinder, but on the opposite side of the window, about a meter distant. At hourly intervals this dish was weighed and returned to its position, a reading of the evaporimeter burette being taken at the same time. The first column of Table IV presents the hourly losses from the burette, for the period from 8 a.m. to 7 p.m., July 28. The second column presents the corresponding losses from the crystallizing dish, while the third column gives the ratio

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*In the spring of the present year the author was able to test the feasibility of obtaining automatic records on such an evaporimeter as the one above described by means of the Ganong (1905) transpirimeter, manufactured by the Bausch & Lomb Optical Company. A perfectly satisfactory record was obtained of the varying intervals at which a gram of water was lost during several days. The instrument is well adapted to this work, but could be greatly improved by being so arranged as to operate without attention for a week at a time.

of the evaporimeter loss to that of 1 sq. cm. of the water surface. In the heading for this column a signifies the area of the dish, 118.82 sq. cm. The different items are for the several hour periods, from 8 a. m. to 7 p. m., on July 28.

TABLE IV.—*Calibration Data for Evaporimeter.*

Loss from evaporation (e).	Loss from dish (d).	Ratio $\left(\dfrac{e\,a}{d}\right)$	Loss from evaporation (e).	Loss from dish (d).	Ratio $\left(\dfrac{e\,a}{d}\right)$
4.0	5.3	89.6	8.3	9.97	98.9
5.4	6.625	96.9	5.4	6.7	95.9
5.5	6.455	101.2	6.2	6.44	114.4
6.5	8.17	94.6	6.6	7.00	112.0
7.2	9.25	92.5	2.4	2.82	101.2
11.1	15.68	84.7	Average	....	99.26

The fluctuations in the ratio are probably in large part due to the failure of slight air currents to accelerate evaporation from the dish as much as they hastened that from the porcelain cylinder; at the beginning of the test the upper surface of the water in the dish was about 7 mm. from the upper edge of the lateral walls. The average ratio for the whole series of observation is 99.26. Other determinations gave coefficients which closely approximated this one. Therefore, in order to save computation, it may be assumed that this evaporimeter lost water approximately 100 times as fast as would a centimeter of free water surface in the same position. In other words, the actual loss of the evaporimeter is taken to be equivalent to the loss from a water surface of one square decimeter.

On the instrument above described readings were taken at convenient intervals from July 24 to August 16. Unfortunately the instrument was not installed until after the beginning of the rainy season, so that a rate of evaporation approaching the maximum for the year was probably not observed. Since reliable records of evaporation are exceedingly rare, and especially on account of the fact that the present observations were made at a station whose atmospheric phenomena are especially interesting to botanists, a table of the daily increments of water loss for the above-named period is worthy of its space here.

Table V presents the daily evaporation and also the rainfall from July 25 to August 22. In the first column are given the dates; in the second, the actual losses of the evaporimeter in cubic centimeters; in the third, centimeters of evaporation, being the loss from a single square centimeter of free water surface, derived from the evaporimeter losses by means of the coefficient 100 above derived; and in the

fourth, the same in inches. The last three columns give the rainfall, in centimeters and inches, and the average temperature (given in degrees Fahrenheit). The latter was obtained by averaging the readings for the day and night separately and taking the mean of these.

TABLE V.—*Evaporation, Precipitation, and Temperatures, Summer of 1904.*

Date.	Evapori-meter loss.	Evaporation.		Rainfall.		Tempera-ture.
	cc.	cm.	Inches.	cm.	Inches.	°F.
July 25..............	129.3	1.293	0.504	0.038	0.015	87.0
26..............	95.86	.959	.374	.038	.015	80.7
27..............	73.60	.736	287	.000	.000	79.4
28..............	116.64	1.166	.455	.000	.000	88.0
29..............	96.40	.964	.376	.000	.000	83.1
30..............	44.50	.455	.174	2.383	.930	80.4
31..............	42.12	.421	.164	1.230	.480	75.1
Aug. 1..............	78.08	.781	.305	.000	.000	77.8
2..............	104.72	1.047	.408	.000	.000	81.5
3..............	101.58	1.016	.396	.000	.000	83.9
4..............	80.60	.806	.314	.589	.230	80.7
5..............	73.65	.737	.287	.000	.000	81.5
6..............	77.15	.772	.301	.871	.340	83.2
7..............	40.40	.404	.158	.179	.070	75.1
8..............	85.90	.859	.335	.000	.000	83.7
9..............	71.34	.713	.278	.000	.000	81.2
10..............	105.26	1.053	.411	.000	.000	......
11..............	105.10	1.051	.410	.000	.000	85.2
12..............	85.60	.857	.334	.000	.000	......
13..............	81.00	.810	.316	.000	.000	82.0
14..............	71.40	.714	.278	Trace	Trace	81.2
15..............	99.75	.998	.389	.000	.000	80.5
16..............	77.78	.778	.303	1.461	.570	77.9
17..............	67.35	.674	.263	.076	.030	74.6
18..............	48.75	.488	.190	.000	.000	77.8
19..............	67.60	.676	.262	1.512	.590	78.6
20..............	57.35	.574	.230	.000	.000	77.8
21..............	46.65	.467	.182	.000	.000	77.0
22..............	38.25	.383	.149	.000	.000	77.0
Total, July 25–Aug. 22......	....	22.642	8.830	8.377	3.270	......

It is interesting to note that from July 25 to August 22 the total evaporation was about 2.33 times the rainfall, notwithstanding the fact that this represents the period of summer rains, and the total rainfall noted is considerably over one-fourth of the average annual precipitation here. The latter is 30.10 cm. (11.74 in.), according to Coville and MacDougal (1903, p. 27).

Observations on the evaporating power of the air can not be made in terms of relative humidity as determined with the psychrometer, for this method, of course, leaves entirely out of account the factor of air currents already mentioned. Perhaps, aside from the evaporimeter

itself, the stationary wet and dry bulb thermometer, placed in an open position where air currents may affect it, is the most reliable instrument for determining evaporating power. Relative humidity computed from readings of this instrument should not be the same as when computed from psychrometer readings, but should bear a closer relation to the losses from the evaporimeter.

The power of air currents to accelerate evaporation was constantly observed in the progress of the work at the Desert Laboratory. This power is noticeable in regard to transpiration from the plant surfaces, as was observed repeatedly in experiments where weighings of potted desert plants were made at short intervals, the plants standing in the open on a shelf near the cylinder of the evaporimeter so that transpiration rates could be compared with those of water loss from the instrument. When the air was quiet the rates of both transpiration and physical evaporation were comparatively low, while the rates rose immediately when even a breeze sprang up and always reached their maxima for any given temperature during the heavy gales which often blew over the hill for hours. It therefore appeared that the transpiration figures obtained by Spalding (1904) by means of the bell-jar method are uniformly far too low to represent nat-
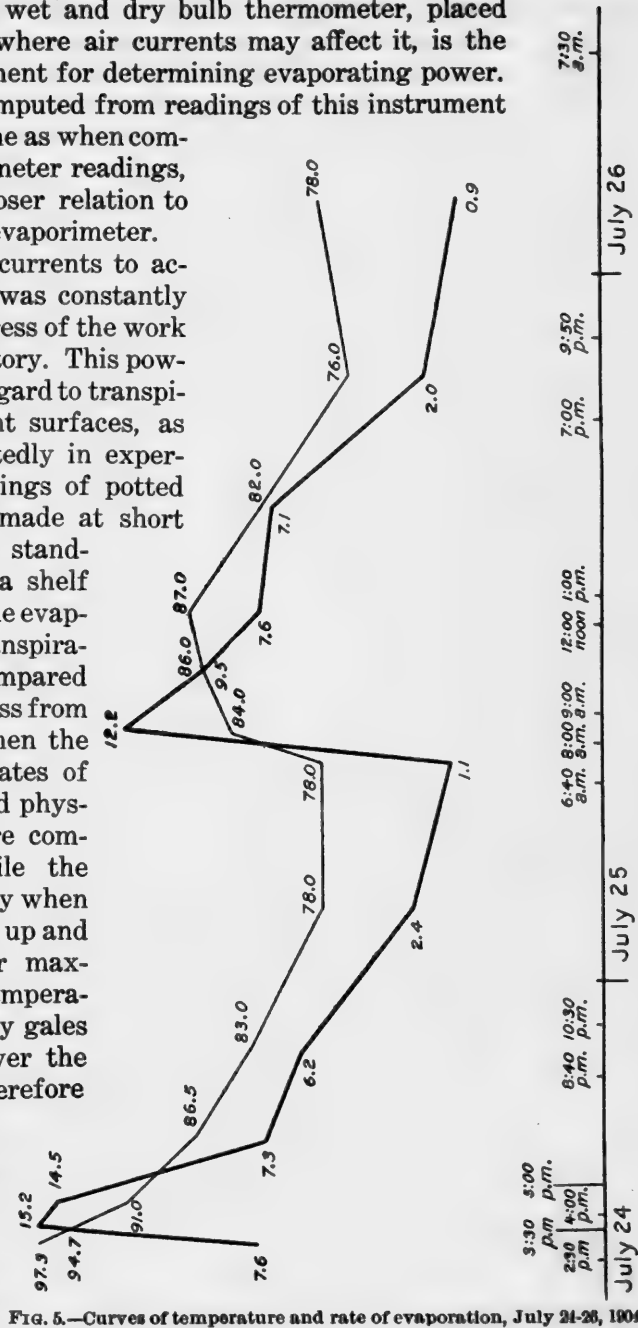
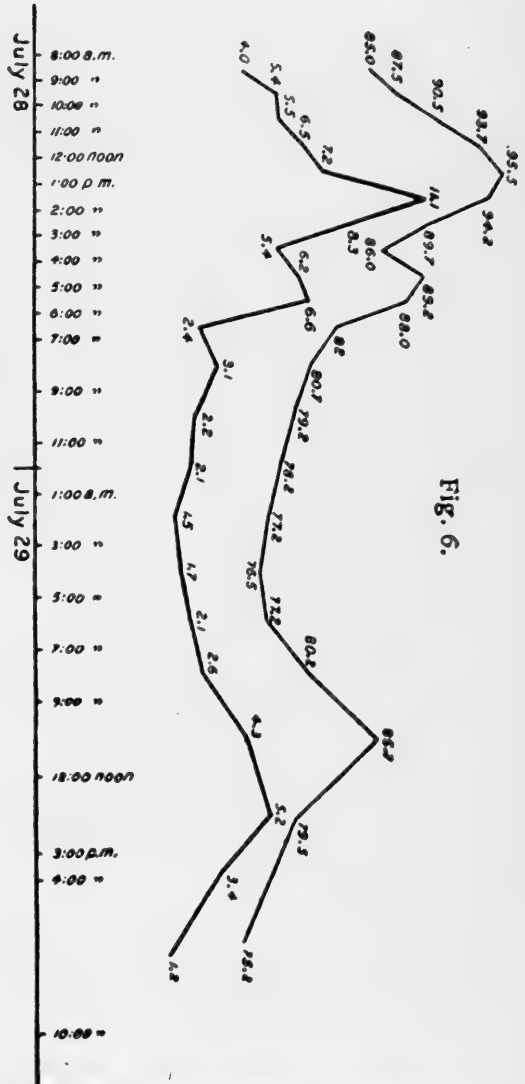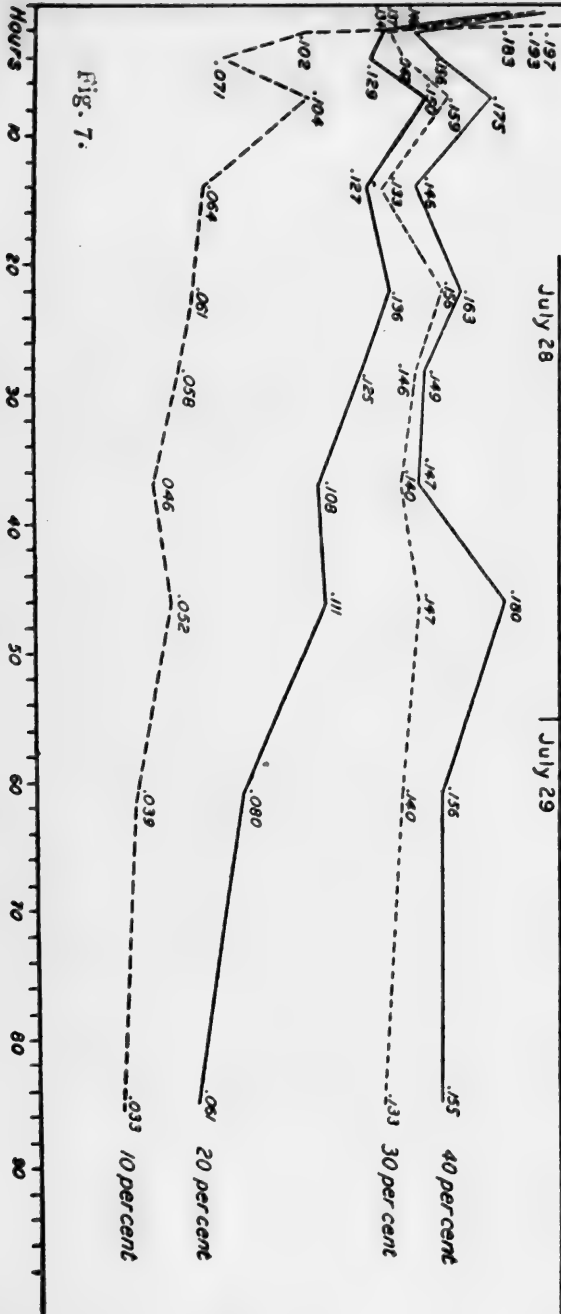FIG. 5.—Curves of temperature and rate of evaporation, July 24-26, 1904.

FIG. 6.—Curve of rate of evaporation, July 28-29, 1904.
FIG. 7.—Curves of rates of evaporation from soils containing different amounts of water.

ural transpiration; the air about the Desert Laboratory is seldom perfectly at rest and then only for short periods.

Curves of temperatures and of evaporation rates were constructed for the period during which the evaporimeter was observed, and these two curves, when brought together upon the same sheet, bring out this point very clearly. During dry gales the curve of evaporation lies much higher in relation to the curve of temperature than when the air was more nearly quiet. Several examples of such rises in rate of evaporation are shown in the portions of these curves given in figs. 5 and 6 (pp. 30, 31). The first of these is for the period from 3 p.m., July 24 to 2^h30^m p.m., July 25, the second from 8^h30^m a.m., July 28 to 7 p.m., July 29. The evaporimeter curve is constructed by plotting rates per hour as ordinates, with time intervals plotted as abscissas. The actual loss for each period is divided by the number of hours, and the resulting average rate per hour is plotted at the middle of the period. Thus different abscissas represent, not the actual times of observations, but the middles of the time periods. The temperature curve is constructed in a similar way, the mean temperature between two readings being plotted with the same abscissa as the rate of evaporation for the corresponding period. The scales are merely chosen so as to bring the two curves into proximity for the whole time of observation. In the figures the broad line denotes evaporation, the narrow one temperature, and the numbers placed near the points on the curves denote, in the one case cubic centimeters per hour and in the other degrees Fahrenheit.

Examination of the curves shows at once that, while in general they both rise or fall at the same time, there are nevertheless many periods during which the direction of change is in the opposite direction in the two, and even where they agree in direction the variations in the two are often by no means quantitatively identical. While many of the minor ones of these independent rises and falls in the curve of evaporation are undoubtedly due to changes in the absolute amount of water vapor in the air, all of the more pronounced ones are to be traced to variations in wind. In figure 4 an extremely high evaporation rate is shown during a violent dust storm which arose about 3^h30^m p.m., July 24, and continued until 6 p.m. A similar high wind arose the following morning about 7^h30^m and gradually fell during the day. The day was cloudy for the most part and a gentle, continuous rain began to fall about 6^h30^m p. m. and continued for an hour or more. In figure 5 the effect of a wind storm is shown between 12^h30^m and 3^h30^m p.m., July 28, and a less violent one on the following day, rising about noon and ending in the heaviest shower of the season, which lasted from 2^h30^m to about 3 p. m. With this shower, as is quite usual, the wind

ceased with the rain and the evaporation rate continued to fall for some time after, not only because of the fall in temperature, but also because of the increase in the moisture content of the air.

Besides the evidence of the curve just presented, the importance of air currents in determining the rate of evaporation may be illustrated by the following comparative measurements. The velocity of the air current produced by an electric fan, when in motion at each of three different speeds, was taken by means of an air meter at a position 30 cm. in front of the fan. Then the air meter was removed and a portable evaporimeter was so placed that its porcelain cylinder occupied the same position. Readings for 5-minute periods were then taken on the evaporimeter, with the air at rest and with three different velocities of air current. Each test consisted of several 5-minute periods. After every test with an air current a test was made in still air, by merely stopping the fan, so as to make absolutely sure that the rate in quiet air had not changed appreciably as time passed. The whole experiment lasted less than two hours and during this time the air temperature remained at 29° C. (84.2° F.), and the relative humidity remained at 63 per cent, as determined by the sling psychrometer. The results are given in Table VI. Air velocities are given in meters and feet per minute and in kilometers and miles per hour; evaporation rates are given in cubic centimeters as observed for 5-minute periods and as calculated for hour periods.

TABLE VI.—*Effect of Wind on Evaporation Rate.*

Velocity of air current.				Evaporation.	
Per minute.		Per hour.		Per 5 minutes.	Per hour.
Meters.	Feet.	Kilos.	Miles.	cc.	cc.
0.0	0	0.00	0.00	0.10	1.2
273.6	900	16.37	10.23	.35	4.2
364.8	1,200	21.82	13.64	.50	6.0
486.4	1,600	29.10	18.19	.57	6.8

This particular evaporimeter was not calibrated by weighing a vessel of water, but since it was similar in every respect to the fixed one which was calibrated, its readings may be taken as approximately equal to the loss from a free water surface of 100 sq. cm. in the same position and during the same period. It is to be noted from the above data that a breeze with a velocity of only 16.37 kilometers per hour produces an acceleration in water loss by evaporation of 250 per cent, and that with an air current moving at the rate of 29.1 kilometers per hour, an accelera-

tion of 470 per cent is produced. No observations of wind velocity on Tumamoc Hill were made, but the air, as has been remarked, is seldom at rest, and strong gales of a velocity probably far surpassing 50 kilos per hour are frequently experienced and often last for hours.*

EVAPORATION FROM THE SOIL.

As has been said already, the surface layers of the soil on Tumamoc Hill are air-dry during most of the year. After a shower they dry out rapidly and in so doing shrink in such a way as to be somewhat loosely porous to a depth of several centimeters. The deep cracks so characteristically produced in many similar soils upon drying from a puddled condition are not prevalent here. Cracks indeed often form, but these are small and close together and seldom penetrate more than a few centimeters below the surface.

The high evaporating power of the desert air removes water from these surface layers much more rapidly than the movement in the soil films can supply it from below, and this soon results in the air-dry condition just noted. Thus the evaporating surface retreats farther and farther into the soil, evaporation being hindered more and more by the thickness of the nearly air-dry layer through which the water vapor must diffuse upward, and finally an equilibrium must be reached where the rate of upward movement of water in the soil films will equal the rate of evaporation. This point is attained in the rock-bound pockets of the Laboratory hill at a depth of less than a meter, as is shown by the actual amounts of water noted in the dry season, and possibly also by the position of the caliche layer, which may mark roughly the position of the average evaporating surface throughout many centuries.

Thus the surprisingly large amounts of water found comparatively near the soil surface even at the end of the dry season are undoubtedly due, as has been already remarked, to the presence of a thick layer of air-dry soil, acting like the dust mulch of the agriculturists. If we suppose a soil to be saturated and supplied with water from below, and if it be supposed to be losing water by evaporation at its upper surface, whether or not a dry mulch will be formed will depend upon the rate of water loss as related to the rate of water movement through the soil. With a sufficiently low rate of evaporation water will be supplied from below as fast as it leaves the upper surface, and therefore during a long period of drought much more water should be lost, and this from a much greater depth, under these conditions, than would be the case if the evaporation rate were high enough to far exceed the rate of water

*On the influence of wind velocity upon the rate of evaporation, see Hondaille (1892, 1 and 2), Russell (1895), and Davis (1900).

movement through the soil films, thus producing a protecting air-dry layer at the surface.   The maximum rate of movement of liquid water through a soil layer depends, first, upon the dimensions of the capillary spaces of the soil, and, second, upon the amount of moisture contained therein.

The comparatively high water content of the humid East or of the Great Lakes region, even during such periods of drought as occur in these regions, produces a comparatively low rate of evaporation, and hence a removal of water from relatively great depths in the soil.   Thus, after several weeks of dry weather the soil of the humid East, where exposed, is probably nearly as dry as the soils of the arid West.   Cameron (1901) and Means (1901) have called attention to the occurrence of true alkali spots in the East, which are evidence of such a condition.   This subject was discussed by Hilgard (1902).   The present author was able to get other evidence in the same direction from the soils of Northern Michigan at almost the same time that the present work was begun.   About June 16, 1904, some two weeks previous to the beginning of the studies of desert soil, a number of soil samples were collected in Kalkaska and Roscommon counties, Michigan, at a depth of about 25 cm. from the surface, and the water content of these was determined.   The highest water content observed at this depth was 15 per cent by volume, in the case of a heavy clay soil covered by a forest of beech, maple, elm, etc., the lighter soils ranging from 2.7 per cent in the case of the sandy jackpine (*Pinus Banksiana*) plains to 10.3 per cent in the case of several loamy soils covered by Norway and white pine (*P. resinosa* and *P. strobus*).   Thus these soils had at that time a moisture content which closely approached that of the clay of Tumamoc Hill at about twice as great a depth and at the end of the spring dry season.   Of course it is to be remembered that, while the desert soil remains at a low moisture content for many months at a time, the content of the Michigan soils must often rise far above these figures after the comparatively frequent rains.   But the evidence is clear that, with the high humidity of the latter region and the accompanying slower rate of evaporation, the soil is subjected to a more rapid drying at relatively great depths than occurs in the arid regions.

Determination was made of the comparative rates of evaporation from the surfaces of several samples of clay from Tumamoc Hill with different water contents.   Only 100 cc. of soil were used in each case, so that the experiment lacks accuracy.   The samples were made up to contain 10, 20, 30, and 40 per cent of moisture by volume, and were placed in Stender dishes 5.5 centimeters in diameter, being tamped into place as uniformly as possible.   Thus the general soil surface exposed

was circular and had an area of 23.76 sq. cm.   The surface was some-
what below the edge of the dish, but this distance was the same in all
cases.   The consistency of the 40 per cent sample was about that required
for modeling clay, perhaps somewhat too moist for such use; the 30 per
cent could still have been used for modeling; the 20 per cent sample was
cohesive under great pressure, while the 10 per cent sample was hardly
cohesive at all.   The dishes stood in the laboratory and were weighed
at frequent intervals, readings being simultaneously taken on an
evaporimeter standing beside them.   In order to eliminate the effects
of variations in the humidity of the air and of such slight air currents as
might occur in the room, the rates of water loss have been calculated
in terms of the evaporimeter rate for the same period.   These rates
are presented in the form of curves in figure 7 (p. 31), the actual
quantities given being the quotients of the rate per hour of evaporation
from the soil divided by the corresponding rate per hour of the evapori-
meter.   These ratios are plotted, as in other cases, at the middle of the
time periods which they represent.

An inspection of these curves shows a curious initial behavior of
the 10 per cent soil.   Its rate at the start was exceedingly high, but it
fell to a position below the other soils within the first three hours.
This is probably due to the fact that in this soil there was not enough
water present to even approximately fill the spaces, so that the actual
evaporating surface was very large, extending down into the soil for
some distance.   As the surface soil dried out the checking of water
loss by the dry soil above became apparent in the rapid fall of the rate,
which continued to fall more and more gradually as the air-dry layer
increased in thickness.   At the end of the experiment 6.95 grams of
water had been lost, or 69.5 per cent of the whole amount originally
present in the sample.

In the case of the 20 per cent sample no such excessively high rate
was observed at the start, there being apparently sufficient water pres-
ent to close the spaces which were filled with air in the 10 per cent
sample.   From the behavior of this curve it appears that with this
water content the soil can transmit water at a rate not very markedly
below the evaporation rate which prevailed at the time, and hence the
air-dry surface layer was very slow in forming.   However, it did
gradually form, and after 22 hours this curve is seen to fall more rapidly.
At the end of the experiment 12.62 grams of water had been lost, or
63 per cent of the amount originally present.

The 30 and 40 per cent samples show little tendency to form air-dry
layers; their curves do not descend markedly, and the rate of water
loss at the end of the experiment is approximately as great as at the

beginning. This must be interpreted to mean that both of these soils were able to supply water from below as rapidly as it was lost at the surface. During the experiment the amount of water lost by these samples was 17.69 grams for the 30 per cent soil and 19.58 grams for the 40 per cent soil, or 59 and 49 per cent of the original moisture content, respectively.

A similar vessel, containing at the start 100 cc. of water, was included in the same series with these soils. Its curve in general follows very closely that of the 40 per cent soil and it is omitted from the figure for the sake of simplicity. The fact above pointed out that the two soils with greater moisture content can supply water as rapidly as it is lost by evaporation is again clearly indicated by the observation that the curve of loss from the water surface is practically coincident with that of the 40 per cent soil. The actual evaporating surface of the soil films is probably larger than that of the water, but this difference is practically overcome by the slower diffusion of the water vapor as soon as the evaporating surface penetrates at all below the surface of the soil.

The average hourly rate of evaporation during this experiment, for each square centimeter of general soil surface, was 0.0055 cc. for the 20 per cent soil and 0.0077 cc. for the 30 per cent soil. Of these two soils the one with the greater moisture content was able to transmit water at a rate at least as great as 0.0077 gram per hour for each square centimeter, while the drier soil could not transmit water at a rate as great as 0.0055 gram per hour, since the latter soil was unable to maintain its average rate, but showed a rate which fell continuously. This point is interesting in connection with the power of the soil to deliver water to plant roots.

PLANT STUDIES.

INTRODUCTORY.

As has been already pointed out, the main physical factor which determines the nature of the vegetation on Tumamoc Hill is the water relation.   Except during the rainy seasons, this soil is far too dry for most plants and only those forms can live here which are adapted to dry soils and high evaporation rate.   In the studies to be here recorded an attempt was made to determine some facts in regard to the minimum water supply with which desert plants can thrive.   Studies of the minimum water supply for germination of seeds were also made.

Since it is next to impossible to make accurate measurements of transpiration and water supply in the case of plants growing in the ground, small plants were grown for the experiments in cylinders of tinned sheet iron, perforated at the bottom to facilitate drainage. Condensed-cream cans, holding from 250 to 300 cc., were found to serve admirably for this purpose.   Some cultures were made in Stender dishes of the form used by microscopists for holding stains, but these lacked drainage and were not as satisfactory as the tins.   Only rain water or distilled water was used for watering the cultures, since the water from the supply tank contains much dissolved salt and the rapid evaporation soon produced a sufficiently high concentration in the soil to injure the plants.

On account of the voracity of the desert animals—insects, birds, and small mammals—it was soon found necessary to protect the cultures by wire netting.   A cage was therefore constructed for this purpose about a meter long, 40 cm. wide, and 50 cm. high, raised about 40 cm. above the level of the ground.   Ordinary mosquito screen of about 3 mm. mesh was used for this purpose.   This cage stood in the open sunshine about 4 meters from the wall of the Laboratory and was thus subjected to uniform weather conditions with plants growing in the ground nearby.

Several different plant forms were chosen for the work, some being extreme xerophytes, others more mesophytic in their nature.   The fact that all work of this kind necessitates potted plants restricted the choice of forms.   It is almost impossible to lift from the soil and pot mature specimens of those desert plants which live through the dry seasons; their roots penetrate far into the soil, through openings between the rock fragments, and can not be removed without injury.

Of a number of the smaller forms with which transplanting was attempted, only a few survived and produced new roots.   One of these was a small plant of *Euphorbia capitellata*.   This is a form with small,

more or less nyctitropic leaves, and stems which extend upward and outward for several centimeters from the summit of a long, woody primary root. It is seldom possible to excavate deeply enough to discover the lateral roots of this plant. It grows and flowers in the driest of situations, is very resistant, and, at most, loses some of its older leaves at times of greatest drought. The small leaves are thick and leathery and do not show the phenomenon of wilting to any considerable degree. When death ensues they simply dry up and still retain their positions along the basal portions of the stems until broken off by external agencies. The plant used lost the main portion of its root system in transplanting, but after about three weeks, during which time the soil was kept well watered, growth had been renewed and the plant appeared quite normal.

Other plants which were transplanted from the ground for these experiments were taken in the seedling condition. At the advent of the summer rains the ground everywhere suddenly becomes almost covered with seedlings of a great group of annual plants which complete their generation in a single rainy season and pass the dry season in the form of seeds. These plants are not especially xerophytic in their structure and appear to be very much like the smaller annuals of more humid regions. Immediately upon germination they send out a long primary root which grows rapidly into the deeper layers of the soil. It is not uncommon to find, a few days after a shower, seedlings of these forms with no development of plumule and only the cotyledons and perhaps a centimeter of stem above ground, while the main root is 10 or 20 cm. in length, still unbranched and growing rapidly downward. It thus comes to be possible for such seedlings to start in the moist soil following a rain and to penetrate within a short period to such a great depth that they are not injured by the rapid and almost complete drying to which the upper few centimeters of the soil are soon apt to be subjected.

The forms which were transplanted to cylinders in the very early stages of their development were a species of *Boerhavia*, about 20 cm. high at maturity, and a *Tribulus brachystylis*, and a single specimen of *Allionia incarnata*. Besides these plants transplanted from the ground, seedlings of *Fouquieria* were grown directly from the seed. Seeds of this plant germinate readily, the two cotyledons becoming green as soon as they reach the light. The hypocotyl elongates rapidly until about 2 cm. long, when this growth ceases and a slow thickening begins. This growth of the hypocotyl continues for two or three weeks, this organ often reaching a diameter of 3 mm. before any development of the plumule occurs. This transverse enlargement is

accompanied by marked hardening of the tissues and by the formation of a true bark. In the meantime the primary root grows directly downward without branching, probably attaining a length in the open soil of many decimeters. In the seedlings grown in pots the roots extended around the base of the pot and finally branched profusely in their distal portions. Not until the root has obtained a remarkable length and the hypocotyl has become enormously thickened and very woody, does elongation of this organ begin again. The plumule, which has been dormant up to this time, then begins slowly to elongate, the first true leaves being produced as much as a full month after the first appearance of the cotyledons.

Several cultivated plants of the more humid regions, such as squash, beans, etc., were also grown from the seed and used for purposes of comparison.

Growth of all these forms, excepting the aerial portions of *Fouquieria*, was exceedingly rapid at this season of the year. The *Boerhavia* and *Tribulus* plants were in full bloom within four or five weeks after their cotyledons appeared. This, it is to be remembered, was during the hottest season. The high temperatures which prevailed seemed to have no deleterious effect upon any of the native plants, nor upon the cultivated plants experimented with, so long as an ample supply of water was provided for the roots, thus allowing the excessively high transpiration to be kept up.

WATER REQUIREMENT FOR GERMINATION.

Seeds of *Fouquieria splendens* were planted in Stender dishes containing soil of several different water contents and note made of their germination. In soils containing 5 and 10 per cent of water by volume the seeds failed to germinate. In the latter soil the wings and outer layers of the seed coat softened and became somewhat like moist paper, but in the former such signs of absorption were hardly perceptible. In a soil containing 15 per cent of water the seeds germinated at last, although germination occurred much sooner in the 20 per cent sample. They germinated earlier in moister soils up to 40 per cent, but were soon destroyed by fungi in 30 per cent and above. It thus becomes evident that, at the temperatures of the summer rainy season, *Fouquieria* seeds require for germination a moisture content in the soil of about 15 per cent, while they germinate and develop well in soils of higher moisture content up to about 25 per cent.

Seeds of *Cereus giganteus* were found to germinate well in 15 per cent soil and with higher moisture content, but soon died with apparent

damping off in soils of 25 per cent or above. It was often noticed that the soil of Tumamoc Hill is full of spores of fungi and bacteria, which develop very rapidly as soon as sufficient moisture is present.

For comparison, a number of seeds of cultivated plants were tested in the same way. Mexican beans (*Phaseolus*) and wheat (*Triticum vulgare*) germinated in 15 per cent and more vigorously in 20 per cent soil. The cultivated balsam (*Impatiens*) germinated slightly in 20 per cent but much better in 25 per cent. Radish (*Raphanus sativus*) failed to germinate in drier soil than 20 per cent. Red clover (*Trifolium pratense*) failed to germinate until a moisture content of 25 per cent had been reached. Thus it appears that of these plants the bean and wheat are able to germinate with as scanty water supply as can *Fouquieria*. Balsam and radish require more water than these, and clover still more. It is probable that the seeds of typically desert plants possess no greater power to germinate in dry soil than many plants of the humid regions. Adaptation to arid climate does not appear to be well marked as far as germination is concerned.

TRANSPIRATION OF DESERT PLANTS.

THE GENERAL PROBLEM.

Whether transpiration is a directly necessary function in plants may be regarded as an unsettled question. By some it is considered as essential in the transport of dissolved salts from the roots where they are absorbed to the upper growing regions, and also in the cooling of green parts when exposed to bright sunlight. By others transpiration is considered as only a necessary evil, an evil because it increases so greatly the amount of water necessary for plant life, and necessary because in order to absorb carbon dioxide from the air, wet membranes must be exposed. This must allow evaporation and thus necessitate a renewal of water to the absorbing surfaces within the leaves. Notwithstanding the emphatic denial by Burgerstein (1904) that there is any reason in the position of Reinitzer (1881), Oels (1902), and Haberlandt (1892), who have expressed themselves more or less definitely as favoring the second of the hypotheses outlined above, the question must not be regarded as settled without conclusive experimental evidence, which Burgerstein is noticeably unable to adduce. So far it seems practically impossible to check transpiration absolutely by inclosing the plant in supposedly saturated air under bell jars and the like, on account of the fact that the absorption of heat by the green leaves must usually raise their temperature slightly above that of the surrounding air. Therefore the only method of experimentation which is available for studying this problem is that of increasing or decreasing transpiration and

determining whether such treatment accelerates or retards growth and the absorption of salts. As far as the writer is aware, no experiments have been carried out with sufficient accuracy to make their results applicable here in more than a general way.

While a certain amount of transpiration may be necessary for plant life in general, it is evident that this does not need to be very great, first, from the fact that the most luxuriant vegetation occurs in the humid tropics and in greenhouses, where transpiration is relatively low, a point brought out by Reinitzer, Haberlandt, and others, and second, from the mere fact of existence of the xerophilous types in which, as is well known, the amount of transpiration is kept very low by structural modifications. It is probably safe to assume that by far the greater portion of the transpiration of desert plants is only a necessary evil. The forms here found are so adapted to xerophytic conditions that their transpiration is reduced to as low a figure as is compatible with the exposure of sufficient surface of moist membranes to secure the necessary carbon dioxide for photosynthesis.

The conditions affecting transpiration in any given plant are, of course, the evaporating power of the air, the supply of water available to the roots, and, to some extent, physiological responses of the leaves, such as the stomatal responses, to changes of light, temperature, etc., and the nyctitropic movements of the leaves themselves. Since the water relation is of paramount importance in all plants, and especially so, as has been already noted, in the forms inhabiting the desert, transpiration becomes probably the most important phenomenon in determining the nature of the vegetation in these regions. Therefore, attention was largely confined during these investigations to measurements of the effect of the three factors mentioned above as controlling transpiration. The results will be given under the two headings, "Measurements of transpiration" (including some discussion of the effect of nyctitropic movements and regulatory phenomena), and "Water requirements."

Some Measurements of Transpiration; A New Method for Studying the Physiological Regulation of this Function.

As has been emphasized above, in order to obtain measurements of the transpiration rate which will most nearly approximate the conditions in naturally growing plants it is necessary to take these measurements in the open air, without inclosing the plant in a chamber. This is to take account of the effect of air currents which have been shown, especially by Unger (1861), to exert great influence on evaporation and transpiration. It is further necessary not to injure the plant in

any way, since the effect of wound stimulus is sometimes great and is always an unknown factor until carefully studied. Thus the potometer commonly used in transpiration measurements is at least of doubtful value until it is tested for each form experimented upon by some other method which does not involve mutilating the plant. On this point see also Curtis (1902).

Furthermore, if the subject of stomatal or other physiological regulation of water loss is to be studied, it is essential that the rate of merely physical evaporation from a uniform water surface be ascertained simultaneously and for the same place with the transpiration measurements. The evaporimeter devised for this purpose has already been described.

The only method which fulfills all the conditions is that of weighing potted plants, the soil of which is so inclosed as to lose no water excepting through transpiration. This method was adopted for the work. Plants which had been lifted from the ground or had come from seed sown in the pots were allowed to grow in the plant cage already described, the soil being kept moist by frequent waterings, until they appeared perfectly healthy and vigorous and had attained a convenient size. Then the pots were sealed up so as to prevent water loss excepting through the plant, and the cultures thus treated were weighed at intervals, readings on an evaporimeter which stood beside them being made simultaneously with the weighings.

For sealing up the pots the composite modeling clay used by sculptors was found to answer very well. It is of about the consistency of putty, adheres with an air-tight joint to all dry solids, hardens very little with age, is readily removed with a knife or spatula when the experiment is finished, and, most important of all, can be applied cold to plant surfaces and has no injurious effect. In short, it is an ideal soft sealing-wax for use in all cases where air-tight and water-tight joints of any kind are to be made and where it is not necessary that the joint bear much pressure. Its cheapness and the fact that it can be obtained from any dealer in artists' supplies, together with the ease with which it can be removed when it has served its purpose, make it much more satisfactory than any of the soft waxes prepared with Venice turpentine, beeswax, etc., with which the author is acquainted.

During the time of the experiment the plant received no addition of water. The soil, of course, became gradually drier and many of the plants finally wilted or their leaves began to wither, showing that they were suffering from lack of water.

At the end of most of the experiments the leaves were removed from the stems and dried in a press. After the writer's return to Chicago the

area of these leaves was determined by making photographic prints of them by contact, on the developing paper known as "velox," cutting out the white portion representing the leaves and calculating the area of this portion from its weight and the area and weight of the sheet. The area thus obtained is, of course, that of one side of the leaves only and must be doubled for the total area. For a full description of this method and data on the uniformity in weight of "velox" paper, see Livingston (1905).

Time was lacking for the determination of these areas at Tucson or they would have been obtained without first drying the leaves. The surface shrinkage, upon drying in the press, of leaves which are not fleshy is, however very slight, not amounting to as much as 10 per cent of the original area in the case of wheat, as the writer has had opportunity to observe. None of the leaves here worked with were of the fleshy type, and thus the error here introduced is probably small. Also, no account was taken of the area of the stems, from which a small amount of evaporation must have taken place. On this point see Burgerstein (1904, p. 27).

In the following paragraphs will be presented the data from the several experiments. These sets of data are numbered in Roman numerals, merely for convenience of reference.

Owing to the difficulty experienced in obtaining suitable pot cultures of those plants which persist in vigorous vegetative condition during the driest parts of the year, only three examples can be given of this class. A single plant of the extremely xerophytic *Euphorbia* already mentioned was available, and the only other plants of the hardier forms which were used were two cultures of *Fouquieria* seedlings, two plants constituting a culture, and each having at the time of the experiment only four or five leaves. All of the other cultures of desert plants were of annuals which appeared only about August 1 and which had practically all ripened their seeds and died by September 7.

In the experiments which are to follow the plants stood either on a shelf near the stationary evaporimeter already described, and were thus mostly in the shade, or on the uncovered portion of the south porch, about 2 meters from the wall of the building, where they had direct sunshine during the day. In the latter case a special evaporimeter stood near them. The evaporation data given in the different experiments are from the appropriate evaporimeter. The plants were taken inside during showers.

Experiment I.—The subject of this experiment was a thrifty plant of *Euphorbia*, in flower at the time. It had been potted several weeks and had apparently entirely recovered from injuries received in trans-

planting. The pot was sealed and the experiment was begun at 12ʰ30ᵐ p.m., August 17, the plant standing in bright sunshine. Weighings and readings of the evaporimeter were made from time to time until 6 p.m., August 19. No wilting or drying of the leaves had yet taken place when the record was discontinued. The data are tabulated in Table VII. In the first column are given the times of observation. Column I_t gives the increment of water loss during the time period just ending, column R_t gives the rate of water loss in grams per hour for that period, and column R_{ta} gives the same rate per square centi-

TABLE VII.—*Data from Experiment I.—Euphorbia.*

[Total leaf area 398.4 sq. cm.]

Date.	Time of observation.	Transpiration.			Evaporation.			Ratio. $\dfrac{R_{ta}}{R_{ea}}$
		Increment (grams). I_t	Grams per hour. Total. R_t	Per sq. cm. R_{ta}	Increment (grams). I_e	Grams per hour. Total. R_e	Per sq. cm. R_{ea}	
August 16	12ʰ 30ᵐ p.m.	......	......	......	......	......	......	......
	3 30	2.2	0.73	0.018	18.3	6.1	0.061	0.030
	6 30	.4	.13	.0003	14.1	4.7	.047	.007
	9 30	.2	.07	.0002	8.6	2.9	.029	.006
	11 30	.1	.05	.0001	2.0	1.0	.010	.013
August 17	5 30 a.m.	.3	.05	.0001	4.7	0.8	.008	.016
	8 30	.7	.23	.0005	4.6	1.5	.015	.038
	11 30	2.9	.97	.0024	10.6	3.5	.035	.069
	3 30 p.m.	3.3	.83	.0021	23.9	6.0	.060	.035
	6 30	.4	.13	.0004	9.5	3.2	.032	.010
	9 30	.2	.07	.0002	6.1	2.0	.020	.009
August 18	7 00 a.m.	.5	.05	.0001	9.4	1.0	.010	.013
	10 00	2.9	1.00	.0025	19.8	3.6	.036	.070
	2 00 p.m.	5.4	1.38	.0045	19.8	5.0	.050	.069
	6 00	1.6	.53	.0014	17.3	5.8	.058	.023
	10 00	.4	.08	.0002	13.2	2.6	.026	.008
August 19	6 00 a.m.	.4	.05	.0001	9.2	1.2	.012	.011
	11 00	4.7	.94	.0024	18.6	3.7	.037	.064
	6 00 p.m.	6.0	.09	.0002	31.5	4.5	.045	.005

meter of leaf surface. Thus R_t is I_t divided by the number of hours in the period, while R_{ta} is R_t divided by the total leaf area. Column I_e gives the increment of water loss from the evaporimeter (approximately equivalent to 100 sq. cm. of free water surface) for the period, column R_e gives the rate per hour, and column R_{ea} gives the same rate per square centimeter of free water surface. In the last column the figures denote the ratio between the rate per hour for unit leaf surface and the same rate for unit water surface. In other words, this ratio shows the fractional part of a square centimeter of water surface which would be required to give off as much water as would evaporate during the

same period and in the same position from a single square centimeter of leaf surface of this plant. This ratio will be termed the rate of *relative transpiration*, the term being used to denote that this ratio shows the relation of transpiration to evaporation.

For the whole period of the experiment, from $12^h 30^m$ p.m., August 16, to 6 p.m., August 19, the average hourly rate of transpiration for the entire plant was 0.420 gram., and the same rate per square centimeter of leaf surface was 0.00105 gram. In order to bring out clearly the manner in which the rates per hour vary during the day, curves have been constructed for them and for their ratio, and these are presented in figure 8. The curves are marked at the left with the symbols which head the corresponding columns in Table VII. Abscissas denote time, dates and two-hour periods being marked on the lower horizontal axis, which is drawn as a broad line for the night periods, from 6 p.m. to 6 a.m. The ordinates are the figures from the table and are placed directly upon the curves. They are plotted at the middle of their respective periods. The two rate curves are plotted on the same horizontal axis and on the same scale for the abscissas. In order to get the curve of evaporation rate into the space allowed, the ordinates for this curve are plotted on a scale only one-fourth as great as that used in the curve of transpiration rate. The horizontal axis for the ratio curve is placed above the other two curves in order to avoid intersections. The scale of the abscissas for this curve is identical with that for the other curves, but the scale for the ordinates is merely one of convenience. A curve of temperatures, arranged by plotting the average temperature for each partial time period at the middle of that period is given with the curve of evaporation rate, this curve being marked *T*. Since weather records are usually made with the Fahrenheit scale a thermometer of this type was used for these observations. The data are given without reduction to the centigrade scale.

It is to be noted at once that the rate of transpiration rises to a maximum in the day period and falls to a minimum in the night, and that the rate of evaporation has similar maxima and minima. This illustrates the commonly observed phenomenon that the rate of transpiration is higher in the day than in the night, and points to the fact that this is largely due to variations in the evaporating power of the air and not mainly, at least, to physiological regulation. It is plain, however, that the two sets of ordinates do not vary at the same rate. This is brought out clearly in the ratio curve, which shows that the rate of transpiration approaches most nearly that of evaporation in the day time and departs farthest from it in the night, although the periods do not coincide exactly with those of light and darkness. This
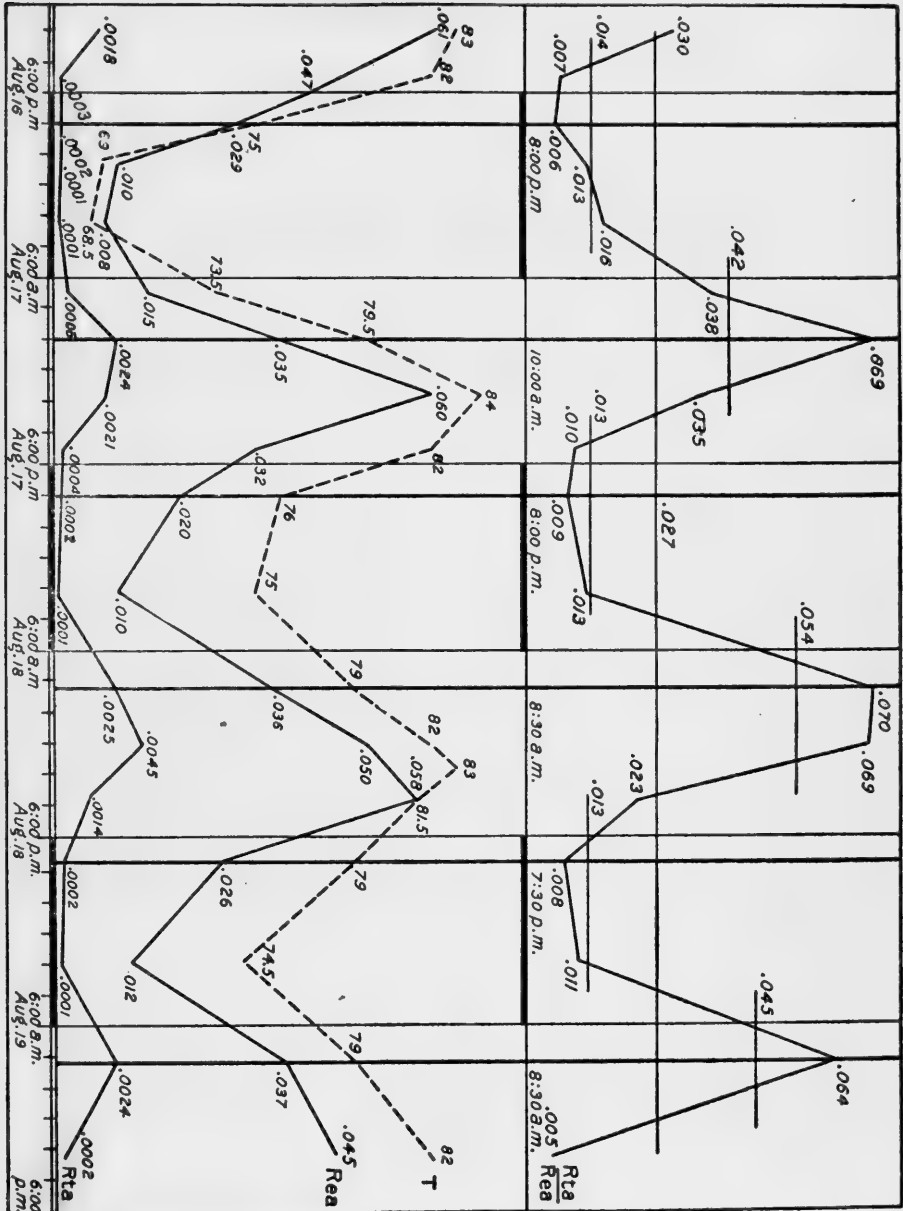
FIG. 8.—Curve of relative transpiration for a plant of *Euphorbia*, August 16-19, 1904. The scale for the ordinates of curve R_{ta} is four times that used for the ordinates of curve R_{ea}.

phenomenon may be brought about to some extent through the action of the green chlorophyl in absorbing heat and thus increasing evaporation from the leaves.   This is probably not an important factor, however, since such rises in temperature can not be very marked.   It is probably brought about mainly by some physiological change in the plant, effective during certain hours, which reduces transpiration to a greater degree than would be brought about by the night conditions of lower temperature and absence of light, as these affect mere physical evaporation.

This physiological activity of the plant is perhaps mainly the response of the stomatal mechanism.*   In this plant it may also be due in part to the nyctitropic movements of the leaves, which, during the hours of darkness or of weak light, fold up closely against the stem and overlap one another so as to decidedly reduce the exposed surface. Lastly, it is possible that the physiological retardation of transpiration may be due to some periodic change in the permeability to water of the protoplasm of the plant tissues.   This might occur in the roots, which, from the experiments of many authors on the subject of root pressure, seem to show a periodicity in absorptive rate, or it might perhaps occur in the mesophyl of the leaves themselves.   No evidence is at hand regarding either of these suppositions.

In order to facilitate the study of these periods of high and low rates of relative transpiration, the average ratio for the whole period of the experiment has been found and has been plotted on the ratio curve as a horizontal line with a constant ordinate equal to the average ratio, which is 0.027.   The average ratio was obtained by merely summing the partial surfaces which are included in the quadrilaterals bounded by each pair of adjacent ordinates, the curve and the axis of abscissas, and then dividing this total area or integral of the curve by the last abscissa, which represents the entire time period of the experiment.   The points of intersection of this line of the average ratio with the ratio curve itself are to be considered as the limits of the physiological periods just noted.   Since no withering of the leaves occurred while these observations were being taken, it follows that the plant did not suffer from lack of water during the period of the experi-

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*Burgerstein (1904, p. 32) agrees with previous writers that the condition of the stomata, whether open or closed, etc., may usually be judged by measurements of the rate of water loss, "denn ist bei einem Blatte die epidermoidale Transpiration gegring, so wird die Grösse der Gesamtverdunstung, die in diesem Falle hauptsächlich auf Rechnung der stomatären Transpiration kommt, bis zu einem gewissen Grade proportional sein dem Öffnungszustand der Spaltöffnungen, so dass man bei relativ hohem (durch Wägung ermittelten) Transpirationswert, auf Öffnung, bei sehr geringer transpiratorischer Leistung auf eine mehr oder wenger vollkommene Clausur der Stomata schliessen kann."

ment. This fact is shown also by the uniformity of the ratio curve itself, and it makes possible the use of this method for determining the average rate of relative transpiration.

The physiological periods cut off by the average line are seen to be fairly regular. They do not, however, as has been already noted, coincide with the periods of solar day and night, but terminate in the vicinity of the hours 3 a.m. and 3 p.m. The period of high rate of relative transpiration falls mainly in the day and that of low rate mainly in the night.

The average ratio for each of the partial periods just described was determined in the same manner as was that for the whole period of the experiment. These ratios are given in Table VIII and are shown on the ratio curve by horizontal lines extending within the limits of the time period which they represent, and having the average ratio for constant ordinate. In the last line of the table are given second averages of the three night periods and of the two complete day periods. Inspection of these data makes it evident that in this case relative transpiration was, in round numbers, three times as great for the day periods as for those of the night.

TABLE VIII.—*Average Ratio—Experiment I.*

Low periods.	Average ratio.	High periods.	Average ratio.
(1) Aug. 16, 2 p. m. to Aug. 17, 4^h30^m a.m.	0.014	(2) Aug. 17, 4^h30^m a. m. to 2^h30^m p.m.	0.042
(3) Aug. 17, 2^h30^m p. m. to Aug. 18, 3^h30^m a.m.	.013	(4) Aug. 18, 3^h30^m a. m. to 3 p.m.	.054
(5) Aug. 18, 3 p. m. to Aug. 19, 4^h a.m.	.013	(6) Aug. 19, 4 a. m. to 12^h 30^m p.m.	.045
Average	.013	Average	.047

A comparison of the rate of evaporation from a free water surface with the transpiration rate from an equal leaf surface was long ago made by Unger (1861), who even went so far as to determine the ratio between the two daily rates, showing that this ratio for *Digitalis purpurea* varied in value, under different weather conditions, from 1 : 7 to 5 : 7. This writer observed the existence of a daily periodicity of absolute transpiration and called attention to the fact that the variations in the rate of transpiration do not follow exactly the variations in the evaporation rate. He regarded transpiration (p. 368), as "ein physikalischer durch die Beschaffenheit der Pflanze modificirter Process."

The only other experimenter who has studied the ratio of the transpiration rate to that of evaporation is Masure (1880), who obtained,

by the weighing method, the ratio of water loss from three vessels, one containing free water, the second containing moist soil, and the third similar to the second but with growing plants of *Xeranthemum bracteatum*. The amount of transpiration was obtained by subtracting the decrease in weight of the second dish from that of the third, the assumption being made that the soil would lose water at the same rate whether with or without plants. This writer's periods of observation were so long, being about a week, that his results failed to bring out the variations in the rate of relative transpiration with which we are chiefly interested here.

A study of the relation of external factors to this physiological periodicity will be instructive. In the first place, it was noticed at once that these periods do not coincide at all with the periods of nyctitropic movement. The leaves were observed to take their nocturnal position between 3^h30^m and 5^h30^m in the afternoon and to return to their diurnal position at about the same time in the morning, while relative transpiration began to decrease, and even to decrease rapidly, several hours earlier in the day than there was any evidence of leaf folding. Thus the leaf movements are shown to be of comparatively little importance in determining the rate of relative transpiration, and stomatal or internal adjustments appear to be the probable controlling factor. This plant transpires mainly from the lower surface of the leaves, and the closing of these organs does not affect evaporation from this surface.

To facilitate the study of the relations existing between external conditions and these variations in relative transpiration, the minimum and maximum points on the curve of the latter have been designated in figure 8 (p. 47) by heavy vertical lines. The lighter vertical lines merely divide the day from the night periods.

A study of the points where the heavy lines intersect the other curves and the axis of abscissas brings out certain interesting facts. Obviously the maximum for the first day of the experiment is not shown. The first minimum is at 8 p.m. Following down the line from this point to the other curves, we find that increase in relative transpiration began at a time when the air temperature was 75° F., and when the evaporating power of the air was such as to produce evaporation from unit water surface at the rate of 0.029 gram per hour. Determining these data for each maximum and for each minimum point throughout the curve of relative transpiration, we arrive at the facts presented in Table IX. This table gives the hour, temperature, and hourly rate of evaporation from unit water surface, together with the maxima and minima of relative transpiration with which they are coincident in time.

TABLE IX.—*Relation of Transpiration to Temperature and Evaporation Rate—Experiment I.*

Minima.				Maxima.			
Hour, p.m.	Relative transpiration rate.	Temperature.	Evaporation rate.	Hour, a.m.	Relative transpiration rate.	Temperature.	Evaporation rate.
		°F.				°F	
8^h oo^m	0.006	75	0.029	10^h oo^m	0.069	79.5	0.035
8 00	.009	76	.020	8 30	.070	79	.036
7 30	.008	79	.026	8 30	.064	79	.037
Average.	.0077	76.7	.025	Average.	.0677	79.17	.036

From these data it appears that the hours at which sudden changes occurred in the general direction of the transpiration curve are not nearly as uniform as are the simultaneous evaporation rates and temperatures. This seems to indicate that either temperature or intensity of evaporation is to be considered as probably the controlling factor in the regulation of transpiration in this plant. From the fact that the hours of the above table fail to show uniformity, it appears that this regulation is not to be related to changes in light intensity nor to any form of chronometric rhythm which the plant might be supposed to possess. Since intensity of evaporation follows temperature rather closely, it is impossible to distinguish between these two factors by the data at hand. Whatever may be its cause, the observed regulation is seen to cause a variation in relative transpiration from a maximum of about 0.068 to a minimum of about 0.008, or from unity to about one-ninth.

The foregoing method promises to be of very great value in studies of the rate of transpiration and of the factors which cause this rate to vary. Indeed, it is the only method so far devised which can give direct evidence in regard to the physiological regulation of transpiration rate. The time necessarily devoted to other lines of research limited the taking of data regarding the relation of temperature and intensity of evaporation to transpiration, so that those here given are necessarily only of a preliminary nature. In the description of the following experiments this matter will be reverted to whenever the data are sufficient to warrant it.

Experiments II and III.—These were brief experiments, carried on in duplicate from 7^{h}30^m p.m., September 4, to 1^{h}30^m p.m., September 5. Each culture consisted of two seedlings of *Fouquieria splendens*. They

stood in the shade near the fixed evaporimeter. Withering of leaves was beginning to be manifest at the time of the second weighing; therefore no more weighings were made. The data for both experiments are given in Table X.

The symbols R_t, etc., of this table have the same significance as in Experiment I. It will be noticed that the hourly rate of transpiration from these plants was 0.839 or 0.83 mg. for unit leaf surface. No data were obtained for the comparative rates of night and day periods.*

TABLE X.—*Data for Experiment II and III.*

	Experiment II.	Experiment III.
Total leaf area...sq. cm...	18.339	14.697
Transpiration, average rate per hour (R_t)..gram.....	.0077	.0061
Transpiration, average rate per hour per sq. cm. (R_{ta}) ....gram.....	.000839	.000830
Evaporation, average rate per hour (R_s).....gram.....	3.58	3.58
Evaporation, average rate per hour per sq. cm. (R_{ea}) ....gram.....	.0358	.0358
Relative transpiration $\left\{ \dfrac{R_{ta}}{R_{ea}} \right\}$	.0234	.0234

Experiment IV.—The subject of this experiment was a thrifty plant of *Tribulus brachystylis* standing in the shade on the north side of the building. It was sealed and the record was begun at 9^h30^m a.m., August 13, and was continued until 8^h30^m a.m., August 15. The total leaf area was 39.69 sq. cm.

This plant has a more marked nyctitropic movement than the *Euphorbia* of Experiment I. The movement consists in the rising of the leaflets of the pinnately compound leaves until their upper surfaces approximate each other, after the manner of the similar movement in *Gleditschia triacanthos.*

The table of fundamental data will be omitted in this and the following experiments, the essential points being brought out clearly by the curves. The curve of relative transpiration for this experiment, together with those of temperature and rate of evaporation, are given in figure 9. These are constructed on the same plan as those of Experiment I.

An inspection of figure 9 shows that during the progress of the experiment the rate of relative transpiration, while showing something

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*Prof. F. E. Lloyd was studying the transpiration of this species especially with reference to night and day rates, while the present work was in progress. His paper on this subject has not yet appeared.

of the periodic rise and fall already described for *Euphorbia*, was, on the whole, gradually decreasing. This is undoubtedly due to the gradually diminishing supply of water in the soil. Wilting did not occur during the experiment, but probably would have been evident had the record been continued an additional day. The average hourly rate of transpiration for the last 24 hours of the record, from 8^h30^m a.m., August 14, to the same hour on August 15, was 0.0723 gram for the whole plant and 0.0018 gram per square centimeter of leaf surface.
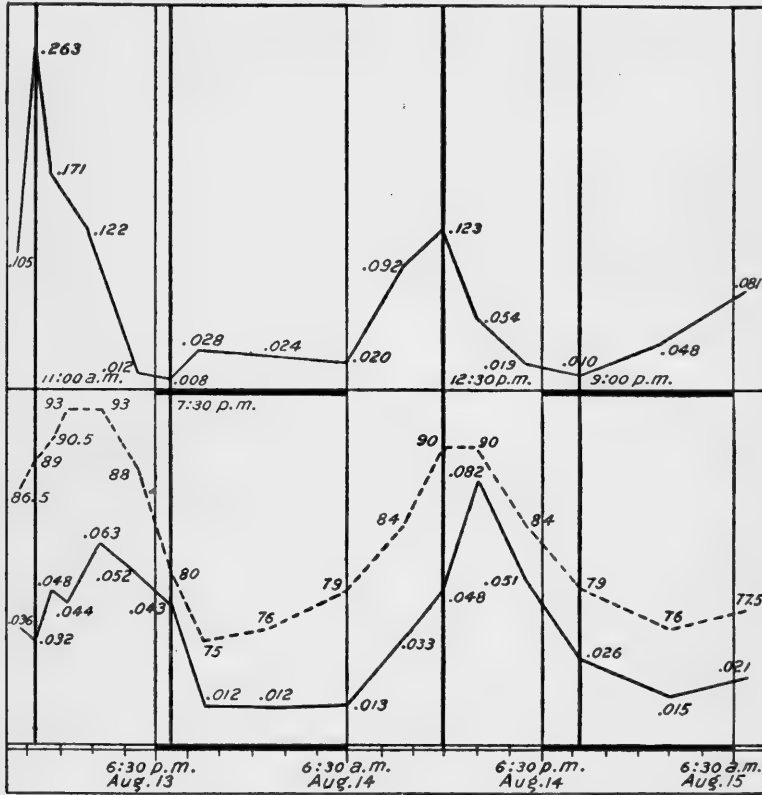

Fig. 9.—Curve of relative transpiration for a plant of *Tribulus brachystylis*, August 13-15, 1904.

As is noted above, this plant exhibits a physiological regulation of the rate of transpiration which is very similar to that of *Euphorbia*. Two maxima and two minima of relative transpiration are shown within the period of the experiment. The comparative data for these points on the curve are presented in Table XI, which is arranged in the same manner as Table X.

An inspection of these data makes it appear that here, as in *Euphorbia*, the hours of the day at which the critical points occur seem to show no uniformity, and therefore the time factor can not be considered as controlling the regulative response. The early hour of the maxima seems again to preclude light intensity. Also, the evaporation rates for the two minima and also for the two maxima are very far from being alike, while the corresponding temperatures are almost identical in each case. Thus it appears that air temperature is the most probable controlling condition governing the regulative response. It is to be noted that the temperature for the maximum in relative transpiration, *i. e.*, the temperature at which the physiological checking of transpiration begins to be manifest, is 10 degrees higher than that which corresponds to the minimum. The latter, is, of course, the temperature at which the check is removed and transpiration begins to increase again.

TABLE XI.—*Relation of Transpiration to Temperature and Evaporation Rate— Experiment IV.*

Minima.				Maxima.			
Hour.	Relative transpiration.	Temperature.	Evaporation rate.	Hour.	Relative transpiration.	Temperature.	Evaporation rate.
		°F	Gram.			°F.	Gram.
7ʰ30ᵐ p.m.	0.008	80	0.043	11ʰ00ᵐ a.m.	0.263	89	0.032
9 00 p.m.	.010	79	.026	12 30 p.m.	.123	90	.048
Average....	.009	79.5	....	Average...	.193	89.5	......

The leaves of this plant were observed to close between 4ʰ30ᵐ a.m. and 6 p. m. and to open between 3 and 4 a. m., thus making it apparent that, while the leaf movement undoubtedly has considerable effect in the regulation under consideration, this movement is not the controlling means by which the regulation is accomplished. Again, it appears that the stomata may be the organs mainly effective in this regard or that some internal adjustment is operative.

Experiment V.—The subject of this experiment was another plant of *Tribulus*, similar to the one used in the last experiment and standing in the same place. The plant was sealed at 2ʰ50ᵐ p.m., August 13, and the record was continued till 8ʰ30ᵐ a.m., August 15. Wilting occurred six hours after the end of the record. The total leaf area was 121.34 sq. cm. The average hourly rate of transpiration during the last 24 hours, from 8ʰ30ᵐ a.m., August 13, to the same hour August 14, was, for the whole plant, 0.3346 gram, or 0.0028 gram per square centimeter of leaf surface.

The curve of the rates of relative transpiration, together with those of temperatures and of evaporation rates, are presented in the same

manner as that used in the previous experiment, in figure 10. As in Experiments I and IV, a periodic fluctuation in the rate of relative transpiration is shown, the low period being in the night and the high period in the day. During the record of the experiment only a single unquestionable maximum is shown. This has a rate of relative transpiration of 0.237 at 6^h30^m a.m., and occurs with a temperature of 79° F.
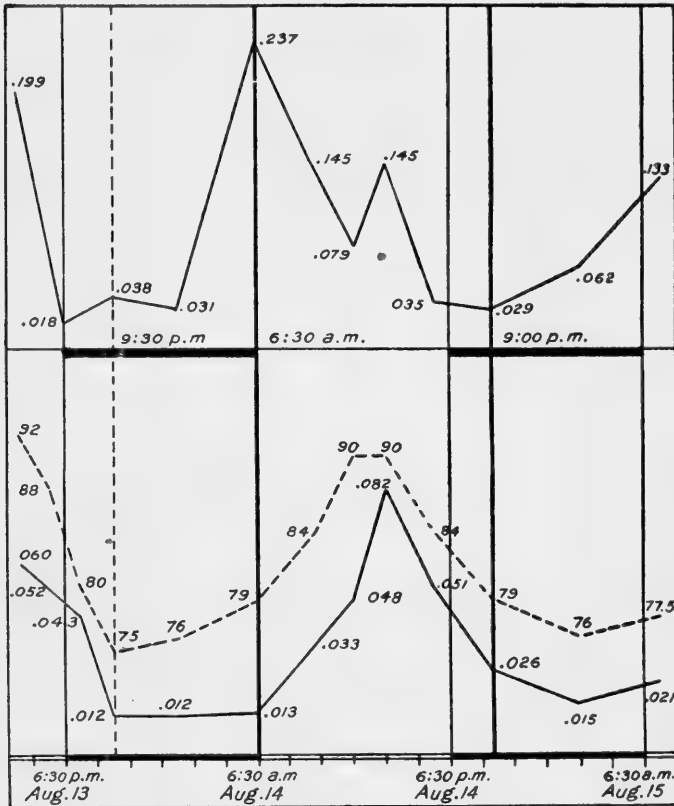

FIG. 10.—Curve of relative transpiration for a second plant of *Tribulus*, August 13-15, 1904.

and an evaporation rate of 0.013 gram. Two minima are shown on the curve, one indeterminate from the curve's form, but probably to be considered as in the vicinity of 9^h30^m p.m., with a relative transpiration rate of 0.038, a temperature of 75° F., and an evaporation rate of 0.012 gram, the other at 9 p.m., with relative transpiration rate of 0.029, temperature of 79° F., and evaporation rate of 0.026 gram. It is to be noticed that in the night of August 13-14 the minimum tem-

perature, as far as the observations show, occurred very early, at 9ʰ30ᵐ p.m. The temperatures at which the two minima occur are much more nearly in agreement than are the corresponding evaporation rates. Obviously light intensity can play no important rôle in the response.

On the whole this curve of transpiration agrees fairly well with that of Experiment IV, and points to the same general conclusion. The variation in relative transpiration in the middle portion of the period of this experiment was from a maximum of 0.237 to a minimum of 0.029, or from unity to about one-eighth, which is the same as in the other specimen of this form used in the last experiment. The present plant had more young leaves than did the previous one, and this fact may explain why its hourly rate of water loss per unit area was higher than in the former case.

Experiment VI.—The subject was a plant of *Allionia incarnata*, consisting of three shoots, each about 15 cm. long, coming from a single root. Flowers were opening during the experiment. The plant was sealed at 11ʰ30ᵐ a.m., August 15, and the record of weighings was continued until 3ʰ30ᵐ p.m., August 17, when wilting ensued. The plant was exposed to bright sunshine during the daytime. The evaporimeter for use in sunshine was not available until 3ʰ30ᵐ p. m., August 16, so that relative transpiration was not obtained till after that time. The total leaf area was 119.44 sq.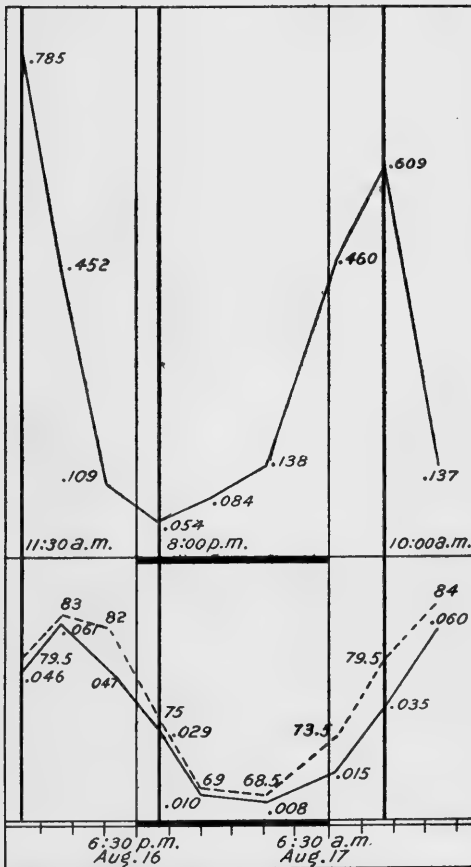 cm., and the average hourly rate of transpiration from the entire plant for the whole period of the experiment was 0.8396 gram, or 0.007 gram per unit of leaf surface. Since the average daily rate of transpiration remains practically uniform throughout the experiment, and does not fall toward its end, this hourly rate may

FIG. 11.—Curve of relative transpiration for a plant of *Allionia incarnata*, August 16–17, 1904.

be taken to represent the conditions just preceding the wilting of the plant.

The curve for rates of relative transpiration and those for temperatures and evaporation rates, for the period following 3^h30^m p.m., August 16, are given in the usual manner in figure 11. Relative transpiration is seen to vary from a minimum of 0.029, at 8 p.m., August 16, to a
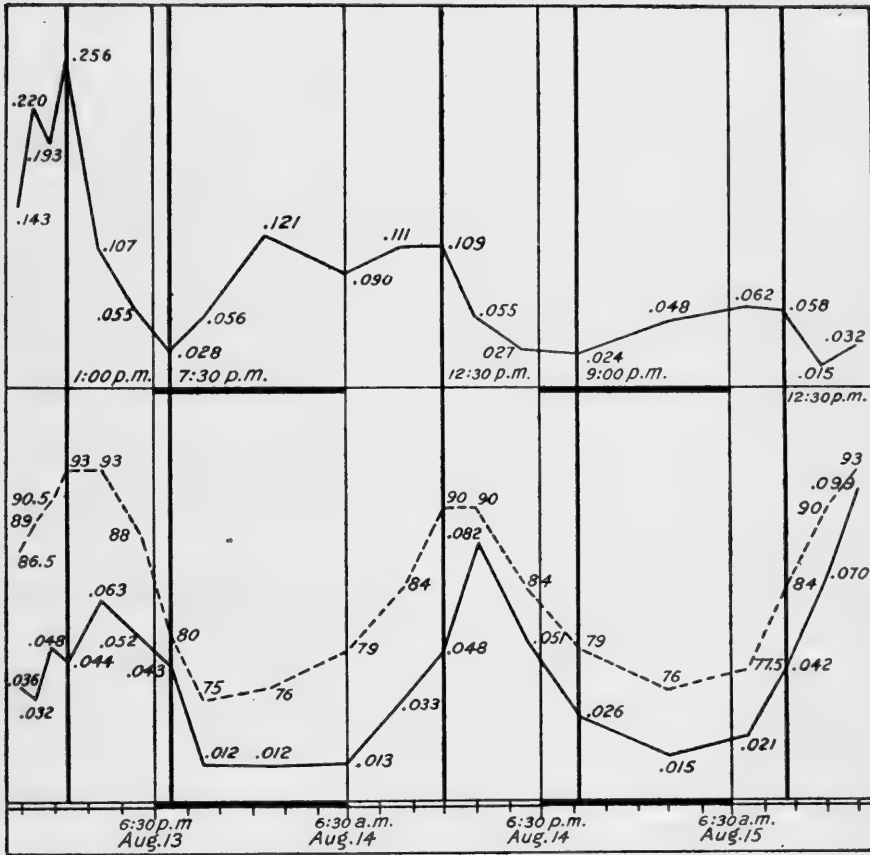

Fig. 12.—Curve of relative transpiration for three plants of *Boerhavia*, August 13-15, 1904.

maximum of 0.371 at 10 a.m., August 17. The minimum occurred with an air temperature of 75° F. and an evaporation rate of 0.029, while the maximum occurred with a temperature of 79.5° F. and an evaporation rate of 0.035 gram. It will be seen that the regulation of water loss causes a variation in relative transpiration from unity as a maximum to about one-twelfth as a minimum.

The period of this experiment was so short that it is impossible to draw any general conclusions therefrom concerning the causal factors which govern the relative transpiration rate. It may be noted simply that the temperature at which the maximum relative transpiration occurred is several degrees higher than that at which the minimum occurred. This plant has no nyctitropic movement and the well-marked regulation of transpiration which is unequivocally shown in the curves is probably due to the stomatal or some internal mechanism.

Experiment VII.—Three *Boerhavia* seedlings were used in this case. They were about 10 cm. high, in bloom at the beginning of the record. The experiment extended from 9ʰ30ᵐ a.m., August 13, to 3ʰ30ᵐ p.m., August 15, when wilting occurred. The total leaf area of this culture was not determined. The hourly rate of transpiration for the last 24 hours was 0.14 gram for the entire plant.

TABLE XII.—*Relation of Transpiration to Temperature and Evaporation Rate—Experiment VII.*

	Minima.				Maxima.		
Hour.	Relative transpiration.	Temperature.	Evaporation rate.	Hour.	Relative transpiration.	Temperature.	Evaporation rate.
		°F	*Gram.*			°F	*Gram.*
7ʰ 30ᵐ p.m.	0.028	80	0.043	1ʰ 00ᵐ p.m.	0.256	93	0.044
9 00 p.m.	.024	79	.026	12 30 p.m.	.109	90	.048
				10 00 a.m.	.058	84	.042

In default of the leaf area a curve of the ratios of the hourly rates of water loss from the whole plant to the hourly rates of evaporation from the whole evaporimeter surface is given in figure 12 (p. 57). This is accompanied by the usual curves of evaporation rates and of temperatures. The ratio curve here given shows, of course, the same variations as would the curve of rates of relative transpiration. The latter curve would be obtained from the ratios of the given curve by dividing each of those ratios by the leaf area and multiplying the quotient by 100, the standard water surface represented by the evaporimeter.

It is apparent from the curve that the rate of relative transpiration decreased on the whole throughout the period of the experiment. Three maxima and two minima are clearly shown upon the curve of relative transpiration. The hours, temperatures, and evaporation rates for each of these are shown in Table XII.

From the data for the two minima it appears that air temperature is probably the external condition which causes the regulative mechan-

ism to act. But from the data for the maxima it appears that evaporation rate is more uniform than temperature and therefore that this is probably the controlling condition for the regulating response. Thus the evidence here is conflicting, much as in the case of Experiment I. Light intensity is again seen to be assuredly not the controlling condition.

This plant has no definite nyctitropic movement, so that here, as in the case of *Allionia*, the variations in relative transpiration are not due to such movement. In the middle portion of the period of this experiment relative transpiration varied from a maximum of 0.121 to a minimum of 0.024. The regulative activity is thus shown to be able to reduce relative transpiration from unity to about one-sixth. It is thus only about one-half as effective in these plants of *Boerhavia* as it was in the two specimens of *Tribulus* and in the *Allionia*.

Experiment VIII. — The plant was a *Boerhavia* standing in bright sunshine during the day. The experiment lasted from 10ʰ30ᵐ a. m., August 16, to 3ʰ30ᵐ p. m., August 17, when wilting occurred. The total leaf area was 47.5 sq. cm. For the last 24 hours before wilting the entire plant transpired at the average hourly rate of 0.2877 gram, or 0.0061 gram per square centimeter of leaf surface.

FIG. 13.—Curve of relative transpiration for a plant of *Boerhavia*, August 16–17, 1904.

The usual curves are given in figure 13. That of relative transpiration is seen to be very similar to the same curve for the *Allionia* of Experiment VI. The first point is probably a maximum, so that here we have to consider two maxima and one minimum. The first maximum is 0.785 and occurs at 11ʰ30ᵐ a.m. with a temperature of 79.5° F. and an evaporation rate of 0.046 gram; the second is 0.609 and occurs at 10 a.m., with the same temperature as
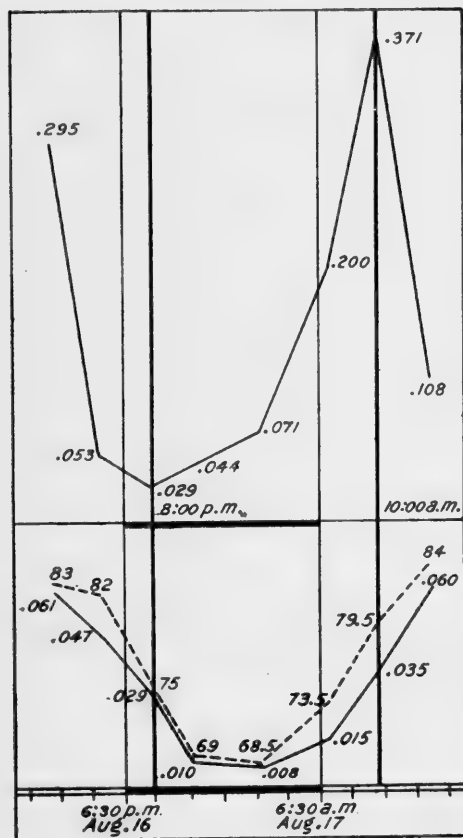
the other and an evaporation rate of 0.35 gram.   The minimum is 0.054 and occurs at 8 p.m., with a temperature of 75° F. and an evaporation rate of 0.029 gram.

It appears here again that temperature rather than intensity of evaporation is possibly the controlling factor in the regulation of relative transpiration, and that the light intensity is not important.   The temperatures for the maxima are again about 10 degrees higher than those for the minima.   The variation in rate of relative transpiration due to
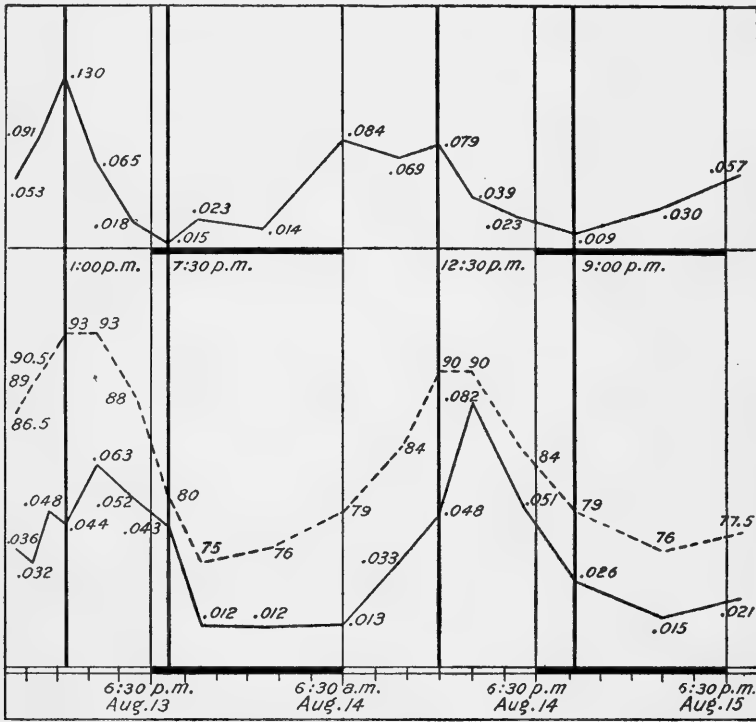

FIG. 14.—Curve of relative transpiration for a plant of *Boerhavia*, August 13–15, 1904.

physiological action amounts here to the difference between 0.054, the minimum rate, and 0.609, the maximum.   Thus the regulative mechanism is able to reduce relative transpiration from unity to about one-twelfth.

Experiment IX.—This experiment was carried on with another mature *Boerhavia* plant, sealed at 9ʰ30ᵐ a.m., August 13.   The record was continued until 8ʰ30ᵐ a.m., August 15, the plant standing in the shade on the north side of the building.   The leaf area was not

determined, but the ratio curve derived from the rates of transpiration for the entire plant is given in figure 14, together with the curve of temperatures and that of evaporation rates for the period. The average hourly rate of actual water loss from the plant for the 24 hours from 8ʰ30ᵐ a.m., August 14, to the same hour August 15, was 0.1340 gram. Wilting did not occur within the time of the experiment.

The curve of relative transpiration shows two maxima and two minima. The hours, temperatures, and evaporation rates for these are shown in Table XIII.

Apparently here relative transpiration is again governed by temperature, and the turning points in its curve are at about 90° and 80° F., the higher temperature once more corresponding to the maximum and the lower to the minimum. The response is effective in reducing relative transpiration from 0.084 to 0.009, or from unity to about one-ninth.

TABLE XIII.—*Relation of Transpiration to Temperature and Evaporation Rate— Experiment IX.*

Minima.				Maxima.			
Hour, p.m.	Relative transpiration.	Temperature.	Evaporation rate.	Hour, a.m.	Relative transpiration.	Temperature.	Evaporation rate.
		°F	Gram.			°F	Gram.
7ʰ30ᵐ	0.015	80	0.043	1ʰ00ᵐ	0.130	93	0.044
9 00	.009	79	.026	12 30	.079	90	.048

Experiment X.—The subject was another flowering plant of *Boerhavia*, standing in the shade. The pot was sealed at 12ʰ30ᵐ p.m., August 16, and the record was continued until 7 a.m., August 18. No wilting occurred. The leaf area was not determined. The average transpiration rate per hour for the entire plant from 9ʰ30ᵐ a.m., August 16, to 9ʰ30ᵐ a.m., August 17, was 0.1729 gram. Curves for this experiment are given in figure 15 (p. 62), following the plan of Experiments VII and IX.

The curve of relative transpiration includes a single minimum of 0.015 at 8 p.m., with a temperature of 75° F. and an evaporation rate of 0.029 gram; and a single maximum of 0.118 at 1ʰ30ᵐ p.m., with temperature 84° F. and evaporation rate of 0.041 gram.

The effect of the regulative response amounts in this case to a difference between a relative transpiration rate of 0.015 at the minimum point and about 0.121 at the maximum. Relative transpiration is thus reduced from unity to about one-eighth.

Experiment XI.—This experiment was carried out with three *Boer-havias* just coming into flower. The record was begun at 6ʰ30ᵐ p.m., August 16, and discontinued at 9ʰ30ᵐ p.m., August 17. The total leaf area of the three plants was 82.6 sq. cm. The average rate of water loss from all three plants for the whole period was 0.7052 gram, or 0.0085 gram per square centimeter of leaf surface. The usual curves are given in figure 16. The period of the experiment was not long enough to warrant any discussion further than to state that a single maximum is shown at about 10 a.m., with a temperature of 79.5° F. and an evaporation rate of 0.035 gram. Minima are not definitely shown within the period.

FIG. 15.—Curve of relative transpiration for a plant of *Boerhavia*, August 16-17, 1904.

Experiment XII.—The subject was a single flowering plant of *Boerhavia* in a Stender dish standing in the shade. The record extended from 6ʰ30ᵐ p.m., August 16, to 9ʰ30ᵐ p.m., August 17. The leaf area was not obtained. The hourly rate of water loss from the entire plant for the whole period was 0.1926 gram.

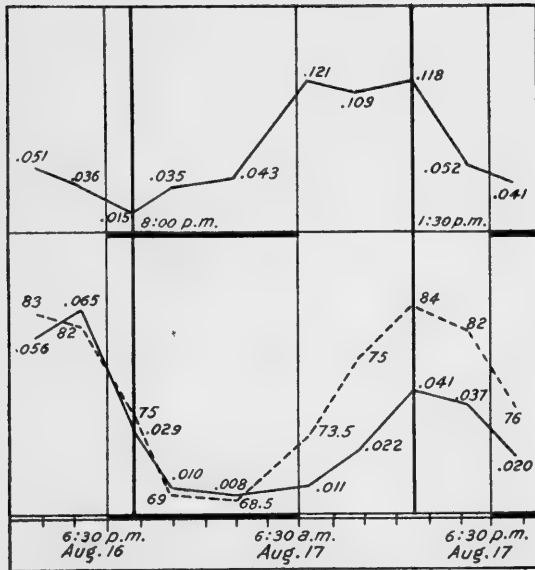The ratio curve for this plant need not be presented. It shows a maximum having a rate of relative transpiration of 0.158 at 7 p.m., with a temperature of 73.5° F., and an evaporation rate of 0.011 gram. Minima are not certainly indicated by the curve.

Experiment XIII.—The subjects were three flowering *Boerhavia* plants standing in the shade. The record extended from 10 p.m., August 18, to 8ʰ30ᵐ a.m., August 21, when wilting occurred. The total area was 63.193 sq. cm. From 6 p. m. August 19 to the end of the experiment the entire culture transpired at the average rate of 0.5860 gram per hour, or 0.0093 gram per hour per unit leaf surface. Only a few weighings were made and a curve could not be constructed.

Experiment XIV.—The subject was a single plant of *Boerhavia* standing in bright sunshine. The record extended from 6 a.m. to

11 a.m., August 19. The plant began to wilt at the last-named hour. The total leaf area was 50.376 sq. cm. During the entire period the plant transpired at the average rate of 1.3620 grams per hour, or 0.027 gram per unit leaf surface. Owing to the short period no curve was constructed for this plant.

Experiment XV.—This test was performed with three seedling squash plants (*Cucurbita pepo*), each having two leaves besides the cotyledons. The soil about them had been kept moist since germination and they had grown with exceedingly great rapidity. The three plants together possessed a total leaf surface of 238.2 sq. cm. They were sealed August 16 at 12^h30^m p.m., and had begun to wilt at 3^h30^m p.m. During this period of three hours they transpired at the rate of 1.9 grams per hour, or 0.008 gram per square centimeter of leaf surface. For this period of three hours their rate of relative transpiration was 0.131.
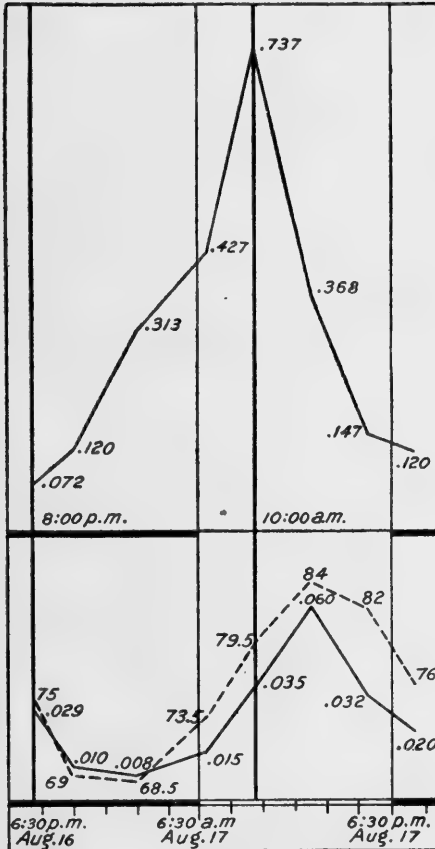
GENERALIZATIONS FROM THE
EXPERIMENTS.

It appears from the data just presented that *Euphorbia*, *Tribulus*, *Allionia*, and *Boerhavia* all show a periodic fluctuation in their relative transpiration. The highest relative transpiration observed was 0.785 (Experiment VIII) and the lowest was 0.008 (Experiment IV). They all have some form of regulative response whereby transpiration begins to be checked between 6^h30^m a.m.

FIG. 16.—Curve of relative transpiration for three plants of *Boerhavia*, August 16-17, 1904.

and 1 p.m., the check being generally removed between 6 and 8 p.m. It also appears that in all three forms stomatal or some internal foliar responses probably play the most important rôle in this regulation of water loss, these being aided perhaps by nyctitropic movements in the first two forms mentioned. As far as the limited data at hand can be

trusted, the temperature of the surrounding air seems to be the controlling condition which governs this regulative response. It seems that when the temperature reaches a certain point in its daily rise the checking of transpiration begins to be effective, and that the check is removed when the air temperature has passed its daily maximum and again decreased to a certain point. The latter point seems, in most cases, to lie somewhat below the point at which the checking response begins. The physiological maximum, at which transpiration begins to be checked, lies, for the forms studied, between 79° and 90° F., and the corresponding minimum, at which the check is removed, occurs between 75° and 80° F. There seems to be no evidence from these experiments for supposing light intensity to be the controlling condition for this regulation, as it is commonly taken to be for most plants,* for the checking of transpiration begins to be noticed too early in the day to be due to diminished light intensity. It is of course possible that with high intensity of illumination the checking of water loss occurs and that this check is removed with the coming on of the nocturnal darkness, but this supposition is the direct opposite of the prevalent idea regarding this regulation. More data are necessary for a test of this point.

There is some evidence that intensity of evaporation is the controlling factor, in some cases at least, but this is not as consistent as the evidence for air temperature. There is practically no evidence from these experiments that the response is due to some chronometric rhythm within the plant. The data at hand do not bear upon the question as to whether this regulation is in any way connected with photosynthesis.

Table XIV presents in tabular form the data obtained as to the relative efficiency of the regulative response. In the first two columns are given the number and subject of the experiment, in the next two the maximum and minimum rate of relative transpiration, as nearly as these can be ascertained. The fifth column gives the efficiency of the regulation of transpiration, being denoted by the ratio of the minimum to the maximum, the former being considered as unity and the latter expressed in round numbers. Thus, in the case of Experiment I, the symbol 1/9 means that the minimum of relative transpiration is approximately one-ninth of the maximum. In the last column the external conditions which apparently control the response are stated, T referring to air temperature and E to intensity of evaporation. It appears from

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*The experimental evidence in regard to stomatal movements and their cause is not very conclusive. For a presentation of the whole subject of the effect of light, temperature, wind, etc., upon the absolute transpiration rate, the reader is referred to Burgerstein (1904). The preliminary character of the present results renders a thorough discussion of the literature unnecessary.

this table that the efficiency of the regulative response varies from one-sixth to one-twelfth, and this without apparent relation to nyctitropic movement; for one plant of *Tribulus*, with marked nyctitropic movement, shows an efficiency of one-twelfth and the other an efficiency of one-eighth, and *Boerhavia*, without appreciable nyctitropic movement, shows a variation in efficiency of from one-sixth to one-twelfth. Further work will need to be done in this field of inquiry before any definite conclusion can be reached.

TABLE XIV.—*Summary of Transpiration Experiments.*

Experiment number.	Subject.	Relative transpiration.		Efficiency of regulation.	Apparent controlling factor.
		Maximum.	Minimum.		
I	Euphorbia......	0.068	0.008	1/9	*T.* or *E.*
IV	Tribulus.........	.193	.009	1/12	*T.*
V	.........do.........	.237	.029	1/8	*T.*
VI	Allionia..........	.371	.029	1/12	......
VII	Boerhavia.......	......	......	*1/6	*T.* or *E.*
VIII	.........do.........	.609	.054	1/12	*T.*
IX	.........do.........	......	......	*1/9	*T.*
X	.........do.........	......	......	*1/8	......

*These efficiencies are obtained from the maxima and minima ratios derived from the rate of transpiration from the entire plant and that of evaporation from the whole evaporimeter surface. See the discussions of the experiments.

A table of the rates of water loss from these plants will be given in the following section, together with data concerning the moisture content of the soil at the end of the experiment.

WATER REQUIREMENT OF CERTAIN DESERT PLANTS.

In the present section will be presented what data were obtained bearing upon the amount of water needed in the soil in order that plants may live in the desert. This problem was attacked directly, by determining the water content of the soil samples in which the plants for the foregoing transpiration measurements had been growing. This was the sole end in view when the first of these experiments were started, the intention being merely to relate the moisture content of the soil to the rate of transpiration both for the entire plant and for unit leaf surface. The data on regulation of water loss, presented in the last section, developed as a secondary consideration in the course of the work.

The results of the moisture determinations of the soils are presented in Table XV. In this table the first two columns again give the numbers and subjects of the experiments. In the two following columns are given average hourly rates of transpiration for entire plant and for one square centimeter of leaf surface, these being calculated

from the last 24 hours of the experiment, or for as nearly that period as was possible from the data at hand. The rates marked with an asterisk (*) in the third column are for plants which had begun to wilt at the end of the transpiration record; in the last column is given the water content of the soil at the end of the experiment, in per cent of its volume under water. These moisture determinations all correspond to soils in which incipient wilting had just occurred.

TABLE XV.—*Relation of Transpiration to Moisture Content of the Soil.*

Experiment number.	Subject.	Average hourly rate of water loss.		Moisture content of soil, per cent of wet volume.
		For entire plant.	Per sq. cm. of leaf surface.	
		Gram.	*Gram.*	
I	Euphorbia	0.4618	0.00115	9.13
II	Fouquieria......	.0077*	.00084	5.50
III	.........do..........	.0061*	.00083	7.70
IV	Tribulus.........	.0723	.0018	10.00
V	.........do..........	.3346	.0028	9.70
VI	Allionia..........	.8396*	.0070	9.50
VII	Boerhavia	.1400*	......	9.05
VIII	.........do..........	.2877*	.0061	10.72
IX	.........do..........	.1340	......	......
X	.........do..........	.1729	......	......
XI	.........do..........	.7052*	.0085	13.70
XII	.........do..........	.1926	......	8.59
XIII	.........do..........	.5860*	.0093	9.20
XIV	.........do..........	1.3620*	.0270	9.90
XV	Cucurbita........	1.9000*	.0080	12.20

It appears from the table that the wilting point for these plants, in terms of moisture content of the soil, lies between 5.5 and 13.7 per cent. It was lowest for *Fouquieria*, intermediate for *Allionia* and *Boerhavia*, and highest for the squash plants of Experiment XV. Judging from the other experiments with *Boerhavia*, the high moisture content of the soil in Experiment XI is probably erratic. This general arrangement of the different plants in regard to their power to withstand a dry soil is what should have been anticipated from their characters. *Fouquieria* and *Euphorbia* are extreme xerophytes, while the squash is a mesophyte. *Allionia* and *Boerhavia*, although they are desert forms, are not active during the dry season, are not markedly xerophytic in their structures.

As has been noted, all of the determinations of moisture content correspond to incipient wilting on the part of the plants involved. In Experiment I this did not occur until 15 days later than the termination of the transpiration record, so that the rate of transpiration given in the table is probably somewhat too high to correspond to the last 24 hours

before wilting. In Experiment IV wilting occurred on the day following the end of the record and the rate is probably not far from correct, while in Experiment V the plant began to wilt only 6 hours after the weighings were discontinued and therefore the rate is very nearly correct in this case. In Experiment XII wilting was manifest 3 days after the end of the record, so that here again the rate given in the table is probably too high. The data at hand do not represent a sufficient number of plants to warrant a critical study of the relations existing between the transpiration rate and the amount of moisture in the soil at the time of wilting. This is a field for another investigation. The problem involves not only the tenacity with which the soil withholds its water from the plant, but also the rate of water movement through the soil from one region to another.

TABLE XVI.—*Moisture Contents of Soils in which Mesophytes Wilted.*

Number.	Name of plant.	Moisture content, by volume.
		Per cent.
1	Vicia faba...	10.73
2	........do..	10.17
3	Phaseolus multiflorus....................................	10.65
4	........do..	10.40
5	........do..	11.62
6	........do..	11.30
7	Helianthus annuus	15.22
8	........do..	13.50

Several other determinations of the moisture content of the soil when wilting occurred were made without transpiration records. Cabbage seedlings wilted July 18 with a moisture content in the soil of 11.10 per cent. Three different soil samples taken August 15 from the root systems of *Boerhavia* plants which were beginning to wilt in the open showed moisture contents of 6.40, 6, and 6.74 per cent, while another sample taken from the root system of a plant which was still vigorous showed a moisture content of 13.6 per cent.

In February, 1905, a number of well-grown potted plants were taken from the greenhouse at the Hull Botanical Laboratory of the University of Chicago and placed in one of the laboratory rooms, where they were allowed to stand without addition of water to the pots until wilting occurred. When this occurrence was noticed soil samples were taken from the midst of the root systems and their moisture contents were determined. The names of the plants and the moisture contents which corresponded with the incipient wilting are given in Table XVI. The soil was a sandy garden soil, containing considerable humus. As

regards the relation of weight to volume in this case, 45.25 grams of dry soil occupied, when allowed to settle under water, 43 cc.

These data are in very good agreement with those obtained for cabbage and squash at Tucson, and probably approximate an average wilting point for most mesophytes.

Of all the determinations made for the wilting point of desert plants only two soils surpassed 10 per cent in water content, these being in the cases of Experiments VIII and XI. It was pointed out on page 11 that the soil of Tumamoc Hill at the end of the spring dry season contained from 5 to 10 per cent of moisture at a depth of only 10 or 12 cm., while, as far as evidence is at hand, it appears that from 12 to 15 per cent of moisture occurred at depths not exceeding 40 cm. Thus it is seen that even in the driest part of the year the moisture content of the soil at a depth of not over 30 or 40 cm. is probably high enough to readily supply such plants as *Fouquieria*, *Euphorbia*, *Tribulus*, and even, perhaps, *Allionia* and *Boerhavia*, with transpiration water. As far as the first three forms are concerned (*Allionia* and *Boerhavia* are not commonly seen here excepting in the rainy season), it seems that these soils are not excessively dry even at the end of the dry season. Such plants as *Brassica*, *Cucurbita*, *Vicia*, *Phaseolus*, and *Helianthus* must succumb to drought conditions somewhat sooner. It was observed in growing the seedlings of squash and cabbage that they required watering several times a day in order to keep them in health, while *Euphorbia* and *Fouquieria* could not only live, but thrive for many days, in a similar vessel of the same soil without watering.

The roots of seedling Fouquierias were often observed to have penetrated to a depth of 10 cm. or more within 48 hours after the first appearance of the cotyledons,* and when it is remembered that the deeper layers of this soil dry out very slowly after being wet by rain, it is easily seen how such seedlings, germinating in the rainy reason, may attain to a depth where they will have a permanent and adequate water supply before the upper layers of the soil have dried out sufficiently to produce death. Seedlings of *Boerhavia* and *Tribulus* are also very active in the elongation of their primary roots, and all of the desert plants studied were characterized by very long tap roots without lateral branches. Although *Boerhavia* thrives only in the rainy season, it was found impossible to lift seedlings of this form more than two or three days after the cotyledons appeared without cutting off their roots. These organs penetrate into the crevices between the rock fragments, so that it is extremely difficult to remove them to a depth greater than from 15 to 30 cm. It appears that plants whose habitats are in the more

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Covillea has the same habit in germination as has *Fouquieria* when the soil is rather dry. See Spalding's figure 3, in the paper (1904) already cited.

humid regions are uniformly not quite so resistant to drought as the desert forms studied. The difference is not very marked, however, and in explaining the existence of desert plants emphasis is apparently to be laid, not upon the greater resisting power of such forms to paucity of soil water, but upon the facts that there seems to be always considerable moisture in the soil under discussion, that this moisture is conserved by comparatively slow transpiration, and that most non-storage forms of the desert root very deeply.

The general conclusions from these studies of the moisture require-ment for the desert forms experimented with are: (1) Those plants which exist throughout the dry season can withstand a somewhat drier soil than those which appear only in the rainy season, and even these latter may often resist wilting in a drier soil than can such non-desert plants as squash, cabbage, etc. (2) There is sufficient moisture in the soil of Tumamoc Hill, and this is near enough to the surface, to supply the transpiration needs of such plants as *Euphorbia* and seedlings of *Fouquieria*. The larger plants of *Fouquieria*, as well as the other shrubs, must be considered as having a root system well enough dis-tributed through the soil to correspond to their comparatively large transpiration surfaces. They probably root very deeply in rock crevices. (3) The roots of seedling Fouquierias elongate directly downward so rapidly as to make it appear possible for them to reach a permanent and adequate water supply before the soil, wet thoroughly by the fre-quent showers of the rainy season, can produce injury through condi-tions of drought. After their roots have reached a depth of 30 cm. the plants are probably safe on the hill in most seasons.

The open formation of desert vegetation doubtless makes it possible for the plants to draw upon a very large volume of soil for their water supply. The noticeable scarcity of seedling or even young plants of the more typical desert forms, even in the rainy season, would seem to indi-cate that conditions other than those of available moisture are effective to reduce the number of these. It may be that in most years the sur-face layers of the soil do not remain moist long enough after each shower to allow the seedlings to obtain a foothold. It seems more prob-able, however, that the depredations of animal life, especially of insects and the smaller mammals, are the most important factor in preventing the growth of seedlings. As has been stated, when young plants are left exposed in the early part of the rainy season, before the desert has assumed the semimesophytic aspect of this season, they are almost sure to be cut off by animals within a day or two. The importance of animal life in determining the nature of desert vegetation is well substantiated by the patent observation that plants which succeed well in arid regions are generally well protected from animals in one way or another.

OSMOTIC PRESSURE OF CACTUS JUICES.

Attempts to express the juices from *Boerhavia* plants and determine their osmotic pressure met with only indifferent success. The sap of these plants is small in amount and very much thickened with slime-like material, so that to express it in adequate amount for the determinations was well-nigh impossible with the available apparatus.

Better success attended similar attempts to determine the osmotic conditions of the juices from the storage tissues of *Echinocactus* and *Cereus*. The storage tissue was cut out in masses, chopped into small pieces, mashed with a mallet, and then strained free from cells and tissue fragments by means of a cloth filter. The extract thus obtained was subjected to freezing-point determinations by means of the apparatus of Beckmann.* The results of this determination are given in Table XVII. Two tests of the freezing-point were made in each case and their averages are used in the calculation of the pressures.

TABLE XVII.—*Freezing-points of Cactus Juices.*

Juice of—	Δ			Pressure, calculated for 25° C.		
	First test.	Second test.	Average.	Atm.	Cm. Hg.	*M.*
Cereus................	°C. 0.420	°C. 0.422	°C. 0.421	5.54	421.62	0.248
Echinocactus	.296	.302	0.299	3.94	299.44	.177

In the table, Δ denotes the lowering of the freezing-point, and the calculated osmotic pressures at 25° C. are given in terms of atmospheres, centimeters of a mercury column, and the pressure of a molecular solution of a non-electrolyte, this being taken as 22.3 atmospheres and denoted by *M*.

A test of *Echinocactus* juice by the boiling-point method gave an elevation of 0.08° C., and a calculated pressure at 25° C. of 3.6 atmospheres, or 274.2 cm. of mercury, which is in very good agreement with the results obtained from the freezing-point.

The osmotic pressure of the cell sap of the cortex of *Cereus* was determined also by the method, commonly used for such purposes, of partial plasmolysis and variation in turgor tension. The epidermis and the underlying storage tissue to a depth of about 5 mm. was removed and cut into strips about 10 cm. long and 5 mm. wide. Owing to the tissue tensions these immediately became concave on the epidermal side, and the curvature was recorded by laying them upon paper and

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*For a description of the methods of freezing and boiling points here used, see Livingston (1903), and references there given, or any book on physical chemistry.

tracing the contour with a pencil. They were then placed in solutions of potassium nitrate of different concentrations and left for half an hour. At the end of this period they were removed and again placed on the tracings which represented their original contour, note being taken as to whether the effect of the salt solution had been to increase or decrease their curvature or to leave it practically the same as at the beginning. Since the epidermal layer is practically nonabsorptive for water and also gives it up with great difficulty, while the cut surfaces of the storage tissue absorb and give out water very readily, an increase in curvature denotes an absorption by the latter tissue and a decrease denotes an extraction of water by the external solution. Thus those solutions which caused no change in curvature are to be regarded as isotonic with the cell sap of the cortex, those in which curvature increased are of lower concentration than this sap, and those in which curvature decreased are of higher concentration. Of course this method is based upon the general assumption that potassium nitrate fails to penetrate the protoplasmic membranes of these cells.

A large number of tests of the form just described were carried out with several different individual plants, and the results showed that the cell sap of the storage tissues just beneath the epidermal layers has a concentration which is equivalent to that of a potassium nitrate solution having a strength of from n/9 to n/5. That is, this sap has an osmotic pressure of from 3.9 to 7 atmospheres. The middle point between these extremes of pressures is very close to the value obtained by the method of the freezing-point, 5.38 atmospheres, so that the two methods are in fair agreement.

Similar tests were made with strips from the flattened internodes of *Opuntia Engelmannii*, and gave n/6 as the approximate concentration of potassium nitrate which is isotonic with the sap of their storage tissues. This is equivalent to about 5.9 atmospheres and is seen to be approximately the same as the pressure found in the case of *Cereus*, but somewhat greater than that found in *Echinocactus*. The osmotic pressures exhibited by these plants are not markedly higher than the author has often observed in the cortex of scapes of *Taraxacum* and stems of *Ricinus* seedlings. It is not nearly as high as that observed by Sutherst (1901) with the freezing-point method in the case of a number of common agricultural plants. This author found, for instance, that the sap of the green stalks and leaves of celery have a pressure of 1,284.25 cm. of mercury. (See in this regard Livingston (1903), p. 85).

All of the cactus juices experimented with contained considerable amounts of mucilaginous material. While such substances do not alter the freezing-point of the solution and probably have no effect upon the

osmotic pressure, they undoubtedly decrease the rate of evaporation. It has been suggested by Aubert (1892) and others that the low transpiration rate observed in the case of the cacti is in part due to the presence of large amounts of organic acids, gums, and slimes in the cell sap of such plants. How important the latter substances may be in *Cereus, Opuntia,* and *Echinocactus* should be well worth a determination.

CONCLUSION.

The most important results of the three lines of investigation already discussed separately will now be brought together. Probably the most interesting fact discovered through these studies is that the deeper lying soil layers of Tumamoc Hill contain at the end of the spring dry season, and therefore probably at all times, a relatively large water content. During the two weeks just preceding the beginning of the summer rains, tests indicated that the soil contained from 12 to 15 per cent of moisture at a depth of not over 40 cm.

This surprisingly large water content of the lower soil layers is probably largely due to the fact that the evaporation rate from the soil surface far exceeds the rate of movement of soil water, thus causing the true surface of evaporation to lie some distance below the soil surface, the water lost finding its way to the air in the form of vapor, which diffuses upward very slowly through the air-dry layers. In this way the deeper portions of the soil are to a great extent protected from loss of moisture by a layer of dry surface soil resembling a dust mulch. The deeper soil layers are doubtless also protected by the presence of numerous rock fragments and by the hard-pan of caliche, which is very slowly permeable to water.

Downward penetration of precipitation water, while it takes place slowly through the soil itself, is on the whole comparatively rapid on account of the oblique rock surfaces, along which movement is not markedly checked.

The amount of soil moisture at a depth of half a meter or less is sufficient to supply the transpiration needs of such typically desert plants as were experimented upon (*Euphorbia* and *Fouquieria*), and is probably also adequate for *Tribulus* and *Allionia,* and perhaps even for *Boerhavia,* the most mesophytic desert form studied. These annuals, however, may not root deeply enough to avail themselves to any great extent of this water.

Seeds of *Fouquieria* and *Cereus* fail to germinate in soils containing less than 15 per cent of moisture by volume, not differing in this respect from *Phaseolus* and *Triticum.* It is thus apparent that *Fouquieria*

and *Tribulus* exhibit no special adaptation to the arid climate of the desert, as far as germination is concerned.

As soon as germination occurs, in *Cereus*, *Fouquieria*, *Covillea*, *Tribulus*, and *Boerhavia*, a very rapid elongation of the primary root sends the tip of this organ far into the soil. While this is taking place the aerial parts grow but slowly. In the case of *Fouquieria* and *Cereus* the cotyledons are the only leaves for many days and even weeks. In *Fouquieria* a curious transverse thickening of the hypocotyl accompanies the rapid root growth, so that after two or three weeks the stem of the seedling is exceedingly thick and woody and is covered with a corky layer, while the root may be still unbranched and may have extended many decimeters into the soil.

This habit of growth is well adapted to desert conditions. During the rainy season the soil is often sufficiently moist for germination, and by the end of the summer the perpetually moist soil of the deeper layers is continuous upward to within a few centimeters of the surface, so that seedlings which exhibit the phenomenon of growth just described should find themselves well rooted in perpetually moist soil long before the drying out of the upper layers could result in their death. It seems that moisture conditions alone can not account for the noticeable lack of seedlings and young plants in the desert, but that the ravages of animal life must play an important part in restricting vegetation.

The clay soil of Tumamoc Hill has a high moisture-retaining power, being able to hold water to an amount about equal to 41 per cent of its wet volume. While this prevents rapid percolation of precipitation water from the surface layers to those more deeply seated, thus keeping much of the water of the first rains of the summer near the surface and thus poorly protected from evaporation, this phenomenon favors water absorption by those storage plants which take moisture mainly from the surface layers of the soil. Mrs. Spalding has noted that when the ground about a *Cereus* plant is moistened, either artificially or by rain, absorption begins almost immediately, long before the water could have reached the deeper soil layers. This must mean that these plants, and probably also the other cacti of the region, absorb water very rapidly from the wet surface soil directly after the rains. Thus the high retaining power of the clay gives to such plants practically all of the water which falls in their vicinity, excepting what is lost by evaporation before they have time to absorb it.

The saps of *Cereus*, *Echinocactus*, and *Opuntia* exhibit osmotic pressures no higher than those commonly found in plants of the humid regions. Therefore, for these cacti at least, adaptation to desert conditions is not manifest in increased concentration of the cell sap.

Experimental data are presented upon the effect of air currents in increasing the rates of evaporation and transpiration, the relative humidity of the air remaining constant. This effect is so marked that methods of transpiration measurements involving the placing of plants in closed chambers, while valuable in studying the physiological condition of the transpiring tissues, must be regarded as giving no clue to the actual amount of transpiration occurring in the open air.

Transpiration studies showed that the rate of water loss per unit of leaf surface is relatively low in the most xerophytic forms studied and somewhat higher in the semimesophytic forms which appear only in the rainy season. A comparison was made between the rate of transpiration and the rate of evaporation from a water surface, with the result that a physiological regulation of the former rate was unquestionably shown to exist. By means of a newly devised form of evaporimeter the hourly rate of evaporation from unit water surface was obtained simultaneously with the hourly rate of transpiration from several different plant forms, for different periods throughout the day and night, and curves were constructed showing the variations in the ratio of transpiration rate to evaporation rate. This ratio has been termed the rate of relative transpiration, and denotes the number of square centimeters of leaf surface necessary to exhibit as great a water loss as was observed, for the same time and place, from a single square centimeter of free water surface.

From the curves constructed for *Euphorbia, Tribulus, Allionia*, and *Boerhavia*, relative transpiration was found to vary from a minimum occurring about 8 p. m. to a maximum between 6^h30^m a. m. and 1 p. m. The highest relative transpiration observed in the experiments was 0.785 and the lowest 0.008. The physiological regulation which this variation shows to exist is not mainly related to nyctitropic movements of the leaves, although these movements may have some auxiliary effect in those forms in which the leaves are nyctitropic. There is slight evidence that the regulatory response is related to evaporation rate, and no evidence at all that the checking of transpiration occurs with diminished intensity of illumination, as is commonly supposed. It is barely possible to explain the phenomenon observed on the supposition that the checking of the transpiration begins when increasing light intensity reaches a certain point and that the check is removed with the removal of light altogether in the early evening; but this supposition is highly improbable and the data at hand are not sufficient to test the question. The supposition that the variation in relative transpiration is due to some chronometric rhythm in the protoplasmic activities of the plant receives absolutely no support from the evidence at hand.

The experimental evidence is very consistently in favor of the idea that air temperature is the controlling factor for the regulatory response in question. It appears that with the rising temperature of the morning hours a physiological maximum is reached at which the rate of relative transpiration begins to be checked, and that this response is reversed and relative transpiration begins again to increase when the air temperature has passed its daily maximum and has decreased to another point which seems to be a physiological minimum. The latter temperature appears to be somewhat lower than the physiological maximum at which the check is imposed. This maximum occurs between 79° and 90° F., while the corresponding minimum occurs between 75° and 80° F.

The regulative response produces a reduction in relative transpiration from unity in the high periods to from one-twelfth to one-sixth in the low periods.

SUMMARY.

The main results of these experimental studies may be briefly stated as follows:

(1) The deeper soil layers of Tumamoc Hill contain, at the end of the spring dry season, and thus probably at all times, a water content adequate to the needs of those desert plants which are active throughout the months of drought.

(2) This conservation of soil moisture is largely due to the high rate of evaporation and the consequent formation of a dust mulch. It is partly due to the presence of rock fragments and of the hard-pan formation called caliche.

(3) Desert forms show an adaptation to existence in dry soil, being able to exist in soils somewhat drier than those needed by plants of the humid regions, but this adaptation is comparatively slight and can not be considered of prime importance.

(4) The downward penetration of precipitation water is slow through the soil itself, but comparatively rapid on the whole, on account of the presence of numerous oblique rock surfaces along which the flow is not markedly impeded.

(5) By the middle of the summer rainy season all of the soil excepting the first few centimeters is sufficiently moist to allow germination and growth of most plants. The surface itself is often wet for several days at a time during the period of summer rains.

(6) Seeds of *Fouquieria splendens* and of *Cereus giganteus* fail to show any special adaptation to germination in soils drier than those needed by the seeds of such mesophytes as *Triticum* and *Phaseolus*.

(7) Immediately following germination, the seedlings of desert plants exhibit a slow aerial growth, but an exceedingly rapid downward elongation of the primary roots, so that these should soon attain to depths where moisture is always present in adequate amount for growth.

(8) The high moisture-retaining power possessed by the soil of Tumamoc Hill holds near the surface much of the water received from single showers and offers excellent opportunity for the rapid absorption of this by such shallow rooting forms as the cacti.

(9) The sap of *Cereus*, *Echinocactus*, and *Opuntia* exhibit osmotic pressures no higher than those commonly found in plants of the humid regions.

(10) The effect of air currents in increasing evaporation and transpiration rates is so great that measurements of natural transpiration can not be made in closed chambers.

(11) By means of a new method involving a newly devised evaporimeter, a physiological regulation of the rate of transpiration was unquestionably shown to exist in the forms studied. The mechanism of this regulation has not been studied.

(12) The regulation of transpiration seems to be controlled by air temperature, the checking of water loss beginning to be effective between 79°. and 90° F., and the check being removed between 75° and 80° F.

(13) The ratio of transpiration rate per unit leaf surface to evaporation rate per unit water surface is termed relative transpiration. Relative transpiration is reduced by the regulatory response from unity in the high periods to from one-twelfth to one-sixth in the low periods.
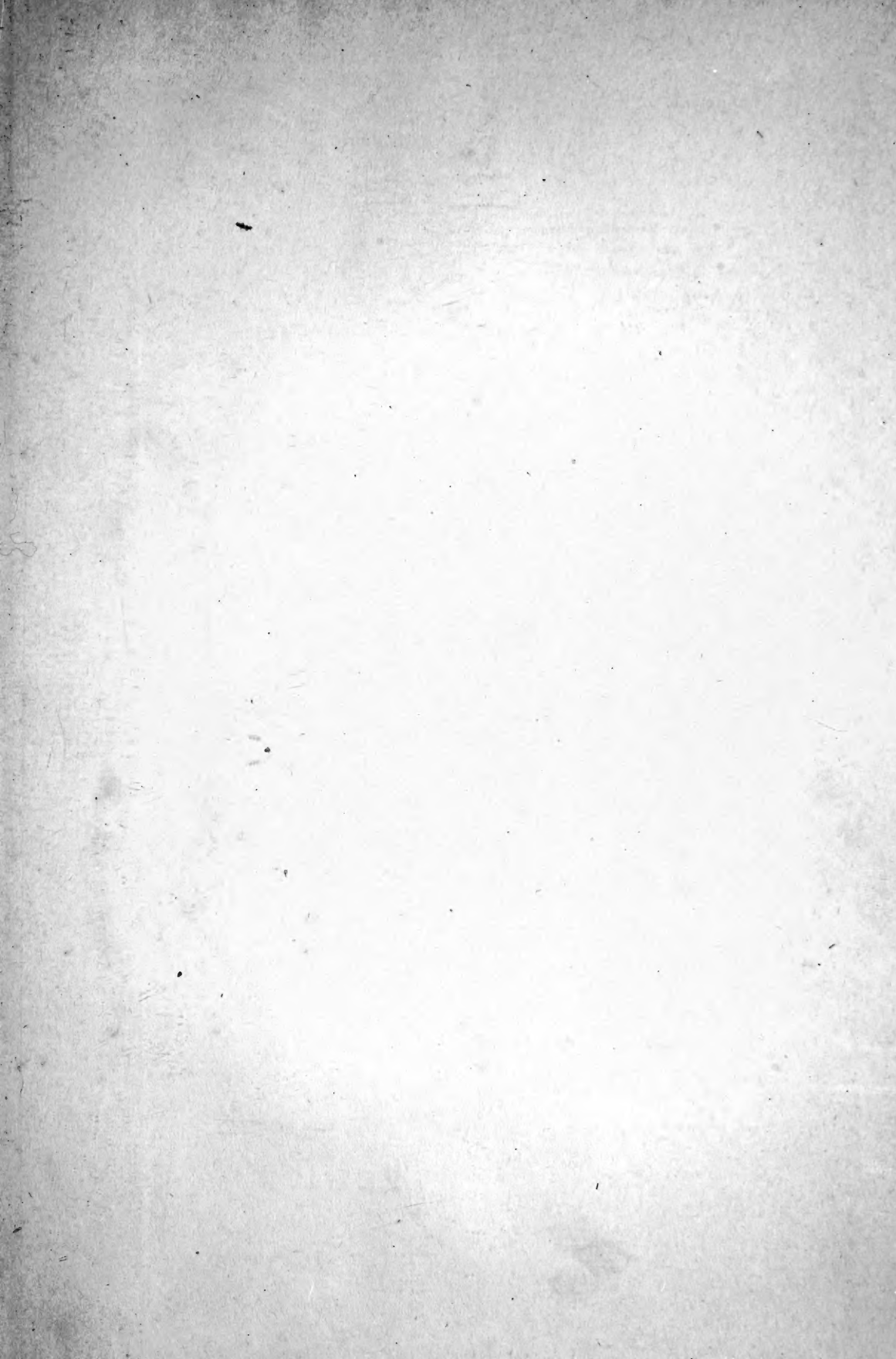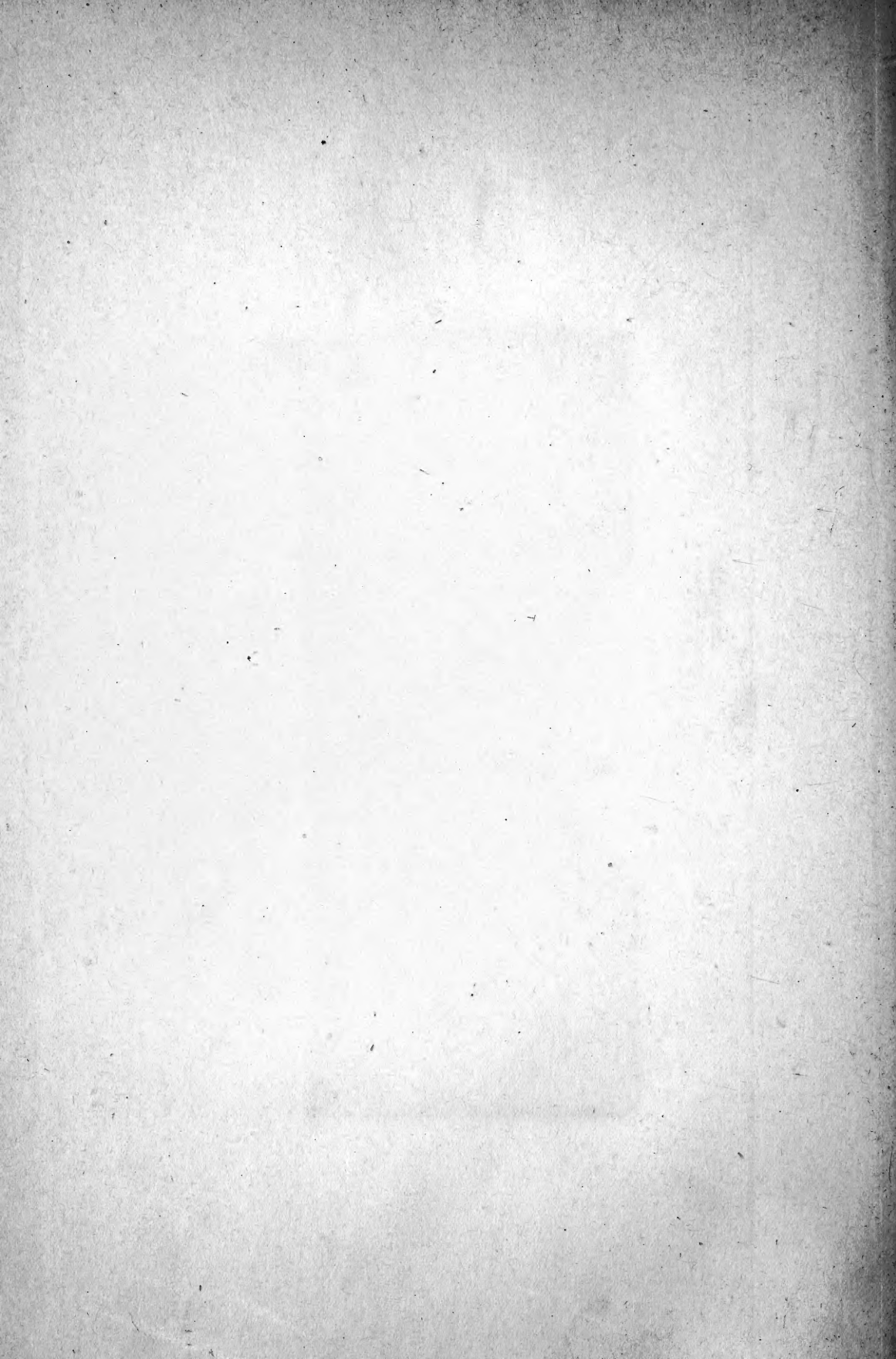
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