The Water-balance of Desert Plants.

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With Plates VI–X.

THE conducting tissues of seed-plants are closely connected with morphologically distensible tracts of medullary and cortical tissue which have an appreciable capacity for the retention of water in plants of even the strictest habit and stature. As the ascending current passes from the absorbent elements to the transpiratory surfaces, some of it may go into such masses of cells constituting reservoirs, in the roots, stems, or leaves. This accumulated supply may be drawn out to the transpiring cells when the pressure of the solution in the cell-sap is overcome.

All plants with massive stems may thus carry a large balance of water, and this stored solution may play a very important part in the life of the individual. The relatively largest balances are carried by some of the species characteristic of the arid regions of the south-western and southern parts of North America, some parts of South America, and the southern part of Africa, while Northern Africa, Asia, Australia, and arid regions in high latitudes everywhere have but few plants with a large water-balance.

The author began some work on the water-balance of desert plants in 1908, and the earlier results obtained have already been published.[1] A few of the plants survived the original tests, and these with other living specimens have yielded evidence upon phases of the subject not discussed in full in the earlier paper.

The Tucson region, in which the observations were made, has a winter rainy season and a wet midsummer, with a hot dry fore-summer and arid after-summer. The total average annual precipitation is about 12 inches. The extremest arid effects are seen in June and early July, when the humidity falls as low as 6 per cent. with midday temperatures of 110° and 112° F. Some of the material was observed in the open, and other specimens were kept in a shaded laboratory room in which the extremes of temperature were not reached by ten or fifteen degrees.

[1] MacDougal, D. T., and Spalding, E. S.: The Water-balance of Succulents. Publication No. 141, Carnegie Institution of Washington, 1910.

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ECHINOCACTUS WISLIZENI.

This species is native to the Tucson region, being found on rocky slopes between 500 and 900 metres elevation. The globose or cylindrical stems attain a length of 1·5 metres and a diameter of half or even two-thirds the length in some instances. The root-system is horizontally disposed.[1] The stems may have a weight of 80 to 100 kg., and the long axes are generally parallel to the axis of maximum illumination, which accounts for a slight leaning to the southward in a perfectly open country. The southern side has the folds more closely drawn together, while the cortex of the shaded side will be more heavily developed with the external ridges of the stem widely separated. The extra weight on the shaded sectors of the plant counterbalances the tendency to fall towards the southward. (See Pl. VI.)

About twenty individuals of various ages were examined during a period of four years. It will be necessary to summarize briefly some of the data already published in order to interpret the newer facts presented.

Echinocactus No. 1. A large plant weighing 42·743 kg. was taken up March 4, 1908, and placed on a suitable support on a platform in a shaded room. The rate of loss at the beginning was 17 g. daily or one part in 2,500, which rose to 29 g. daily in the arid fore-summer, dropped to 14 g. during the summer rains, rose to 18 g. in the dry after-summer in September, and then fell irregularly to 1 g. daily in December. This rate of one part in 40,000 is the lowest recorded for any plant that came under observation. The highest daily rate, one part in 1,100, was observed in May, 1908. A year later, when the plant had lost about 4 kg. or 10 per cent. of its original balance out of a total weight of nearly 43 kg., the daily rate was but one in 2,500 of the total weight. With reference to the amount of the water-balance, the daily rate was one in 1,300 in May, 1908, and one in 2,000 in May and June, 1909, at which time the weight was about 38 kg.

Echinocactus No. 2 was taken up November 5, 1908, and placed in the room with No. 1, weighing 5·136 kg. The midwinter rate of loss was as great as that of No. 1, but it soon fell to 0·6 g. daily. This was equivalent to one part in 8,056. The plant was placed in an equable temperature room in mid-February in which the thermometer showed a rise from 56° F. to 71° F. in midsummer, and the humidity ranged from 80 to 90 per cent. The rate under such circumstances rose to 0·7 g., seemingly independent of humidity, with a direct relation to the temperature at first, but the rate continued to increase despite the falling temperature until it reached 1·3 g. daily in October. A decrease now ensued parallel to the falling temperature which carried the rate down to 0·27 g. daily, or one part in 18,000.

[1] See Cannon, W. A.: The Root-habits of Desert Plants. Publication No. 131, Carnegie Institution of Washington, 1911.

Late in February, 1910, the plant was removed to the open and the rate immediately rose to 6 g. daily, and with the coming of the arid fore-summer rose to 21 g. daily, or one part in 150 of the weight at the beginning of the period taken into account. The rate now fell to 7 g. in the rainy season, 3 g. in October, 1910, 1 g. in November, and 0·5 g. in December to February, 1911, or one part in 5,000 of the total weight. The loss in December to February, 1908–9, was one part in 3,000 of the water-balance and about one part in 4,000 of the water-balance two years later (1910–11). The weight on March 20, 1911, was 2·220 kg., showing a loss of 2·916 kg. or 56·5 per cent. of the original weight in the total period of desiccation extending over thirty months.

A chemical analysis of the plant made in April, 1911, showed total solids of 8·097 g. per 100 c.c. of sap, and 3·149 g. of ash, with an average osmotic activity of 2·3 atmospheres at 25° C. This plant, as well as No. 3, may be supposed to have reached the limit of endurance, and disintegration had set in, although a high concentration of the sap contents had not been reached.

The record of this plant includes some data of importance as bearing on the capacity of such plants to absorb moisture through their aerial surfaces. The weight in the open on February 28, 1911, after a drizzling rain lasting through the night, was 2·430 kg., which was 8 g. more than on February 20, 1911. The loss during the eight days would have been about 4 g., so that an estimated absorption of 12 g. by the spines and external structures must have taken place. The plant showed no adhering drops or films of water, and the weighing was done at noon on the 28th.

Echinocactus No. 3 was taken from the soil on March 6, 1908, and placed on a base of loosely-piled black volcanic rocks in the open, its estimated weight being 5·480 kg. It weighed 3·893 kg. when brought into the laboratory on November 5, 1908, and during the next month gained 14 g., which may be attributed to absorption of water vapour by the dead and dried spines. The daily rate of loss was 0·8 g., or one part in about 5,000 in the period from November to February.

The plant had now been deprived of a water-supply for a year, and when placed in the soil exhibited the usual phenomena of growth and flower formation during the summer of 1909. The roots were embedded in soil in a suitable box and the preparation set under a glass shelter without sides, an arrangement which would allow desiccation to proceed as usual. The plant was freed from the soil on November 5, 1910, cleaned, and the roots cut away to simulate the conditions in November, 1908, and the weight was found to be but 4 kg., showing that practically all accretion of dry material had been used in the construction of roots, although some expansion of the head had taken place in 1909. Still supported under the shelter, but separated from its roots and soil, the rate of loss was 1·6 g. daily from

November, 1910, to February 3, 1911, or one part in 2,500, the glass shade having been removed. Its weight was 3·855 kg. on February 28, 1911, and after a rain of 0·19 inch in the form of a slow drizzle throughout the night, the same weight was found. Estimating the total loss at the rate in the preceding period, it must have amounted to 40 kg. in twenty-five days, and this amount appears to have been balanced by the absorption on the part of the dried spines and other external parts. It may not be asserted that any of the above absorption was carried on by living tissue, nor does it appear that the water taken up might be of use to the plant.

The chemical analysis of the sap in April, 1911, showed 9·512 g. solid matter per 100 c.c. of sap and 3·864 g. of ash, the average of over a dozen determinations giving an osmotic pressure of 2·2 atmospheres at 25° C. The total solid and ash were thus about five times the minimum shown by a turgid plant (see p. 76). The concentration of the sap was greater than that of any plant previously examined, yet it is notable that the osmotic activity was scarcely more than half that of any other specimen examined. This would seem to indicate that actual disintegration had begun, and that this individual might not have been able to recuperate if supplied with soil moisture.[1] The total loss was 2·075 kg. or 36·2 per cent. of the original weight in three years.

Echinocactus No. 4 was taken from the soil, the root-system cut away, and placed on a base of loosely piled volcanic rock in the open on March 5, 1908. The estimated weight was 1·192 kg., which was reduced to 795 g. on November 5, 1908. A slight gain in weight was noted, as in No. 3, when this plant was brought into the shaded laboratory. The rate of loss was 0·5 g. daily in the 164 days ending May 21, 1909. This was equivalent to one part in 1,500. The rate was 0·6 g. in August, then fell to 0·4 g. and to 0·2 g. in November, and then during the midwinter period fell to 0·13 g., or one part in 5,300. A gain of 2 g. in weight ensued when the plant was placed in the humid dark room for seven days. The humidity was 62 per cent. with a temperature of 58° F. Upon being taken out the rate rose to 0·4 g. in March and 0·6 g. in May, which was practically equivalent to the rate at the corresponding period of the previous year. A rate of 0·4 g. was maintained from July to November, when it fell during the period of November to February to 0·11 g., or one part in 5,000, which, with corrections for variation in periods of observation, is not materially different from the rate of the year before.

The room in which this plant was placed was heated during February so that the rate rose to 0·24 g. daily and the weight fell to 549 g. on February 28. It was now placed outside for four days, its final weight on March 5, 1911, being 549 g. It was then set on the parapet wall of

[1] See MacDougal and Cannon: The Conditions of Parasitism. Pub. 129, Carnegie Institution of Washington, p. 33, 1910.

the laboratory. The high temperatures and intense sunlight soon killed it, however. (See Pl. VII.)

Echinocactus No. 6 was taken from the soil November 7, 1908, and after being freed from roots was mounted on a stand in the laboratory. The initial net weight was 28·573 kg., and the rate of loss during the first month was 13 g. daily, which was about one part in 2,200 of the total weight. The rate during the winter fell to 0·6 g. daily, or one part in 5,000, and rose in the hot fore-summer to 10 g. daily. By October, 1909, the rate had fallen to 8 g. daily, and to 2·5 g. daily in November, which was one-fifth of the rate of the previous year. The rate in January was 1·7 g. daily, or one part in 16,000. Observations now showed 2·2 g. in March, 4·6 g. in April, 6 g. in May, 7·2 g. in June, 7·7 g. in July, 5·8 g. in August, 5 g. in November, and 2 g. daily in the period extending into February, 1911, a rate of one part in over 12,000, which was greater than that of the previous year, but was still less than the rate of loss during the first year of observation. The rate increased to 2·6 g. daily during February as the room was heated daily during that time. The rate of loss during the first seventeen days of March was nearly 4 g. daily, and 2·3 g. daily during the twenty-four days ending April 10. The entire loss during twenty-nine months was 3·713 kg., or nearly 13 per cent. of the original weight. No noticeable growth had taken place, but sixteen greenish-yellow fruits were retained. It is to be seen that the changes in the form of this plant would be such as to maintain fairly constant transpiratory conditions, and the variations from year to year are to be ascribed to other causes than variations in temperature, air currents, &c.

Echinocactus No. 7 was taken from the soil November 7, 1908, freed from its roots, and set on a metal support in the laboratory. The net weight was 35·818 kg., and the rate of loss during the first month was 18 g. daily, or about one part in 2,000, which was slightly more than that of No. 6. The rate during the winter was 10·5 g. daily, or one part in about 3,500, which was higher than in No. 6. The rate ran very irregularly, falling to 8 g. daily in June, 9 g. in August, and decreasing to 4 g. in November, which, like that of No. 6, was much less than in the previous year. The winter rate did not fall below this, however, and amounted to one part in over 8,000, which was double the rate of No. 6. The loss rose to 9·8 g. daily in June, fell to 6 g. in August to October, to 4 g. daily in October, while the midwinter rate, 1910–11, was 2·1 g. daily, or one part in 15,000, less than that of No. 6 and slightly less than its own rate of the previous year. The rate from February 3 to February 28 was 1·6 g. daily, a notable decrease and less than that of No. 6 during the same period. The erratic record from February to April was found to be due to errors caused by a mouse's nest built among the arms of the balance. During the next seventeen days the rate rose to 2 g. daily, and to 3·3 g. daily during the twenty-four days ending April 10, 1911.

The weight was now 31·570 kg., the total loss during the entire period of the experiment extending over twenty-nine months being but 42·48 kg., or less than 12 per cent. of the original. During this time some apical growth had ensued and eighteen fruits were retained. This plant, with No. 6, was set up for further observation.

Echinocactus No. 10 was taken from the soil November 7, 1908, freed from its roots, and set on a tin box near the south side of the laboratory in the open. Its net weight was 14·588 kg. and it lost 61·6 g. daily during the first month, or one part in 220, about ten times the rate of plants in a shaded room. The rate during the next six months was 30 g., the total being 4·860 kg., out of the original noted above. This rate was one part in 430, which is about five times that of Nos. 6 and 7 during the same period in the shade.

The analysis of the expressed juice of the sap of the cortex gave the following data :

Specific gravity	1·035
Acidity calculated as H_2SO_4 per 100 c.c. . . .	0·1064
Total solids per 100 c.c. of sap	7·060
Ash content of sap per 100 c.c.	3·009

A similar analysis of a turgid plant taken up on September 9, 1909, gave the following :

Specific gravity of sap	1·0095
Acidity calculated as H_2SO_4 per 100 c.c. of sap . .	0·0887
Total solids per 100 c.c. of sap	2·092
Ash content of sap per 100 c.c.	0·792

Echinocactus No. 13 was taken from the soil and freed from its roots on February 18, 1910, after which its net weight was found to be 49·390 kg. It was now mounted on a base of loosely piled black volcanic rock near a *Carnegiea* taken up at the same time. Definite points were located for calibration, and the greatest length was 585 mm. and the greatest diameter 413 mm. The rate of loss was 150·5 g. daily from February to May, this being one part in over 300 total weight. The total loss of 12·490 kg. up to May 12, 1910, was accompanied by a decrease in length of 25 mm. and of diameter amounting to 43 mm. The rate of loss fell to 102 g. daily in July, some new spines being formed and flower buds developed at this time. The rate fell to 33 g. daily by October 3, 1910, at which time the total loss was 12·845 kg. This rate amounted to one part in 873. Although the plant had lost over one-fourth of its total water-balance, eighteen flowers had been formed and eight small fruits matured. The length had decreased to 500 mm., a further shrinkage of 60 mm. in length and of the diameter to 325 mm., a loss of 45 mm. The lowest rate, 9·3 g. daily or one part in nearly 2,900, was found in the period of thirty-five days ending November 9,

1910. The rate rose to 14 g. daily during the period ending February 6, 1911, and the external dimensions remained unchanged from the measurement of October 5, 1910. During this period of eighty-nine days the external measurements did not follow the transpiratory loss.

The final weight, taken on March 20, 1911, was 25·540 kg., indicating a total loss of 455 g. in forty-two days at the rate of nearly 11 g. daily. The total loss in thirteen months amounted to 23·850 kg., or 48·3 per cent. of the total weight. The total solids in the sap amounted to an average of 3·7 g. per 100 c.c., the ash being 1·4 g. per 100 c.c. The average of a large number of freezing-point determinations gave an osmotic activity of about 3 atmospheres at 25° C. These results show a different aspect from anything previously examined. The plant seemed alive as indicated by its osmotic pressure, but the soluble matter in the sap had been reduced to a minimum.

Some interesting relations appear when the amount of loss is contrasted with the degree of succulency. Turgid specimens of *Echinocactus* contain 90 to 95 per cent. of their total weight in water, and this plant may be estimated to have contained about 45 kg. of water at the beginning of the experiment. The cylindrical body, with its fluted surface, offers about twice the transpiratory area of a plain cylinder of the same measurement, which would amount to about 15,000 sq. cm. The degree of succulence would, therefore, be about 3 or 3 g. of water present to each sq. cm. of surface. This is to be compared with 10 g. in leaves of *Suaeda* as determined by Miss Delf.[1] In this condition the plant lost in the open one part in 300 on the average during a period when daily temperature ranged from 32° to 90° F., and in the full blaze of the desert sunlight.

The total loss in weight up to May 12, 1910, was 12·490 kg., which may be taken as being principally water, the total amount remaining now being about 32·5 litres. The surface had shrunken to 14,000 sq. cm., but the succulence had also decreased to about 2·3. These conditions, together with the higher relative humidity prevalent in July, were seen to result in a lessened rate of loss during the summer. At the end of the dry after-summer, the surface showed a further estimated decrease to about 3,000 sq. cm., and as but small loss had ensued since the last observation, the total now being 12·485, the remaining water may be estimated to have been about 32,000 litres, which indicates a succulency of 2·4 g. per 100 sq. cm. of surface, which is slightly greater than that shown in midsummer, although the rate of loss was much lower. Other factors may be taken as contributing to this result. The approximated position of the folds and the cooler night temperatures would both tend to lessen the rate of total loss. Next it is to be seen that as soon as the transpiratory loss was not taken up by the changes in external dimensions, the rate increased even under the retarding

[1] See Transpiration and Behaviour of Stomata in Halophytes, Ann. of Bot., vol. xxv, 1911, pp. 485–505.

influence of seasonal factors least favourable to transpiration. Nothing may be safely said as to the cause of this rise. It is to be noted in this connexion, however, that the amount of dissolved solids in this plant, instead of being about seven or eight parts per hundred, as shown by other desiccated specimens, was about half this amount, not very much more than the proportion shown by a turgid specimen. The disintegration of certain substances in the walls of the cells or membranes may have altered their permeability and permitted a more rapid water loss.[1]

The Tree Cactus *Carnegiea gigantea*, Britton and Rose, or Sahuaro forms a trunk 25 to 50 cm. in diameter with a heavy cylinder of woody tissue, enclosing a medulla of a diameter amounting to 8–10 cm. in some instances. The cortical layer of colourless cells is also very thick, the outer layers of this tissue being chlorophyllose. Externally the trunk presents a series of longitudinal folds or ridges, separated by furrows which vary in depth much more widely than similar structures in the various species of *Echinocactus*. The older portions of the trunk may become so distended as to eliminate the folding or plaiting. The trunk may reach a height of 12–15 metres and bear many heavy branches. The total weight of the larger plants might be estimated at 2–4,000 kilos, 85–90 per cent. of which may be taken as water. The water-content may, however, undergo a wide variation, as is well illustrated by the following paragraphs.

The root-system penetrates the soil more deeply than those of the *Echinocactus*, and even these organs are thick, soft, and contain a great amount of fluid.

Carnegiea No. 1 was taken up May, 1908, and freed from soil and roots, after which it was set in a perpendicular position on a base of loosely piled rocks in the open. Its estimated weight was about 40 kg. November 5, 1908, the weight was 32·518 kg. It was now brought into the laboratory with the Echinocacti already described. Water was lost at a rate of 62 g. daily during October, and at the rate of 23 g. daily during the next six months, which amounted to one part in 1,700 of the weight at the beginning of the period. The analysis of the expressed juice obtained from the terminal portion of the trunk gave the following results :—

Specific gravity	1·0355
Acidity calculated as H_2SO_4 per 100 c.c. of sap	0·103
Total solids per 100 c.c. of sap	9·622
Ash content of sap per 100 c.c.	2·754

Carnegiea No. 1 *a* was taken up, freed from soil and roots, October 22, 1909, when it weighed 45·325 kg. It was suitably mounted in the laboratory, and lost weight at the rate of 114 g. daily during November. This

[1] The transpiratory mechanism of *Echinocactus* has been described by Cannon. See Biological Relations of Certain Cacti, American Naturalist, vol. xl, Jan. 1906, p. 27.

rate fell to 8 g. in January, 5·5 g. in February, and rose to 67 g. daily when removed to the open in May, June, and July. The rate fell to 6 g. daily in October, 1910, and to 3·8 g. in the period of 89 days ending February 6, 1911. The loss during a part of February, 1910, was one part in over 8,700, while in the corresponding period of a year later it was but one part in over 9,300. The last calculation was made for a longer period, and the actual minimum may have been much lower.

The total weight of the plant was reduced from 45·325 kg. to 34·810 kg., a total loss of 10·535 kg., or 23·3 per cent. of the original weight. The chemical analysis made in April, after some further loss had been undergone, showed the following :—

Total solids in juice per 100 c.c. . . .	10·44 g.
Ash content of sap per 100 c.c. . . .	1·83 g.

Three determinations of the osmotic activity by the freezing-point method gave 10·15, 9·64, and 9·72 atmospheres, the average being 9·84 atmospheres at 25° C.

Three analyses of growing plants previously reported [1] show total solids in the juice ranging from 3·4 g. to 5·9 g. with an ash content of 1 to 1·7 g. per 100 c.c. of sap.

The desiccation of this plant, which had progressed without any repletion of the water-balance for over 16 months, may be taken as representing about the limit of endurance of the species without water, both as to time and amount of loss. It is of interest to note also that determinations of the osmotic activity of the sap of individuals rooted in moist soil by the freezing-point method gave pressures of 6·78 atmospheres, although some as low as about 4 atmospheres by plasmolytic methods are on record.[2] It is to be seen from this that the range of variation with regard to this condition is as 1 to 2.

The desiccation of *Carnegiea* was not found to cause any noticeable reduction in length, a fact that may be readily understood when the heavy woody cylinder is seen to be well formed to within a few centimetres of the upper end of the trunk. The shrinkage in the cortex would result in some decrease in diameter, but this would be accomplished by contraction of the folds without any great decrease of the outer surface. Turgid trunks consist of over 90 per cent. water, but their slender cylindrical form would operate to give them a relatively lower succulence than *Echinocactus*. Furthermore, the degree of succulence would be much lowered during desiccation by the maintenance of the surface area as suggested. Transpiratory loss seemed to be more or less closely correspondent to the succulence, and to be

[1] In Publication No. 141, Carnegie Institution of Washington, 1910, p. 47, 1911.

[2] See MacDougal and Cannon : Conditions of Parasitism in Plants. Pub. 129, Carnegie Institution of Washington, 1910, p. 25.

affected by the seasonal changes in an obvious manner. No changes of mode or discontinuity in the rates of loss, such as were seen in *Echinocactus*, were recorded. The extremest stages of desiccation were accompanied by highly increased total solids and ash content of the sap.

Carnegiea seedlings. Twenty young plants, seven months old, were taken from the flat in which the germinations had taken place, and put in a dish in the laboratory, November 4, 1910. The net weight of the lot was 27·244 g., and the loss during the first three days was 6·865 g. at the rate of 2·286 g. daily, this being one part in 12 of the total. Much of this may be attributed to the desiccation of the exposed root-surfaces, although all of the finer branches had been removed. The rate of loss was 0·5 g. daily, or one part in 40 during the next nine days, while in the next 79 days ending February 3, 1911, the rate was 0·85 g. or one part in 30, an increase for which no adequate cause may be given. February 24, 1911, the net weight was 12·499 g., the loss in the preceding 21 days having been 0·055 g. indicating a rate of one part in 46. The total loss was 14·745 g. or 54 per cent. of the original weight. Four of the seedlings were wilted beyond revival, and as many more were in a doubtful condition, the above may be taken as roughly representing the average resistance of the seedlings. From this it may be seen that the seedling loses water at such a rapid rate during even the cooler season as to exhaust its effective balance in about 100–120 days. The death of some of the individuals ensues when something less than 54 per cent. of the total water-balance is lost. This is, however, a greater degree of endurance than that exhibited by adult plants, as may be seen by reference to page 79. The older individuals are not able to withstand a loss greater than about 23 per cent. of their original turgid weight.

Thirty-six resting corms of a native *Brodiaea* were taken from the soil on October 30, 1910, and brought into the laboratory to obtain data which might be of interest in comparison with those furnished by the seedlings of *Carnegiea*. The net weight of the lot was 46·7 g., and the loss during the first 24 hours was 4·9 g., which was one-eleventh of the total. This doubtless represents the desiccation of the outer dried coating of the bulbs. The loss during the following day was 0·78 g. or one part in 53. During the next week, ending November 9, 1910, the loss fell to 0·31 g. daily or one part in 130. The loss during the week ending November 16, 1910, was 1·680 g., 0·24 g. daily, or one part in 200. The total loss was 18·425 g. or 39·5 per cent. of the original weight during 96 days. During the latter part of this period young corms were developed, and the contents were slowly withdrawn from the older ones. The desiccation of the other structures described in this paper resulted in depletions in water-balance followed by shrivelling and contraction of the affected members. The reaction of *Brodiaea*, however, is seen to consist in the formation of new smaller corms which are plump and turgid, although each one contains but the fraction of the water of the larger member from which it originated. The repetition of this action might result in the survival of the species through several arid seasons by the seasonal development of a series of diminishing size (Pl. IX, D).

IBERVILLEA SONORAE.

The indurated tubers of this plant are irregularly globose or flattened, and lie on the surface of the ground. A network of small fibrous roots is formed during the summer rainy season and serves to take in a supply of solution which is added to the enormous balance already present. The growing points which are distributed irregularly over the surface of the tuber awaken at the same time, and produce vines which may reach a length of two to three metres, quickly maturing flowers and fruits (Pls. VIII and X). The rhythm of the plant is such that this activity ensues for many seasons after the plant has been separated from the substratum, as has already been described.[1]

A tuber of a plant which had been established at the Desert Laboratory in 1906 was taken up October 22, 1909, and when cleaned and freed from roots and dead vines, weighed 530 g. The loss was 0·4 g. daily during the first 15 days, or one part in 132, 0·16 g. daily in the next 12 days, and in the 51 days ending January 8, 1910, the loss was but 0·08 g. daily or one part in 6,500. The rate fell to 0·04 g. daily in the latter part of January and February, which was but one part in nearly 13,000, but rose to 0·11 g. daily during the 55 days ending April 21, 1910.

The rising temperature stimulated the formation of green stems in May, the rate of loss rising to 0·3 g. daily, or one part in 1,500. The rise continued until the rate was 0·08 g. daily in July, which was one part in 573, this being the greatest transpiratory activity exhibited at any time. A decrease now began which brought the rate to 0·05 g. in the period ending October 3, 1910, and to 0·3 g. in November, after the vines had died. The rate during the following 91 days was 0·09 g. daily, or one part in nearly 4,500, which it may be seen is in excess of the rate during the corresponding period of the previous year. The room containing this plant was warmed in February so that the rate increased to 0·16 g. daily, the weight being 389 g. on the last day of the month. The rate during the first 20 days of March was less than 0·1 g. daily, decreasing slightly during the next 21 days, but rising again to exactly 0·1 g. daily during the 20 days ending May 1, 1911, slightly less than the rate of loss during the corresponding period in 1910.

May 26, 1911, the weight was 387 g., indicating a daily loss of 0·12 g. during May, an increase commensurate with the higher temperatures prevailing.

[1] MacDougal, D. T.: Botanical Features of North American Deserts. Pub. No. 99, Carnegie Institution of Washington, 1908, p. 20.

The total loss from this plant in 19 months was 143 g. or 27 per cent. of the total weight. This included the material used in the construction of stems and leaves in the summer of 1910. In addition to the increased transpiration from these stems, some marked loss would be attributable to respiration and to the falling away of dead stems and branches. (See upper right-hand figure in Pl. X.)

Ibervillea Nos. 4 and 5 were received as freshly collected tubers from Dr. J. N. Rose, who was in the field near Guaymas, Sonora, in March, 1910. The tubers were cleaned and freed from roots, then placed on suitable supports in a shaded laboratory. The weight of No. 4 was 1·452 kg. on March 17, 1910. The loss during the first five days was 25·6 g. daily, which was about one part in 520. Much of this accelerated loss was due to the transpiration from cut surfaces and bruised tissues. With the closure of such places the rate fell to 1·3 g. daily in April, and 0·85 g. in May, although the rising temperature would have tended to increase the rate, which continued to fall until it was but 0·36 g. in June, which was one part in nearly 3,700. The development of a number of branching stems caused the rate to rise to 0·66 g. daily in July, which fell to 0·5 g. in the period ending in early October, when the stems were dead. A decrease continued which brought the rate to less than 0·2 g. daily in late October, and to 0·04 g. daily in the period ending February 3, 1911, which was but one part in 30,000. The room was warmed to 18° C. for a few hours daily during February, and the rate of No. 4 rose to 0·3 g. daily in March, but fell to 0·05 g. daily in the 20 days ending April 10, but rose to 0·35 g. in the 21 days ending May 1.

May 26, 1911, the weight was 1·260 kg., indicating a daily loss of 0·16 g. in May, which was less than that in April, although green stems were being formed. A similar decrease in the rate of loss was recorded for the corresponding period of 1910 as noted above. No explanation may be offered for the erratic behaviour of this plant, which was kept within a few centimetres of the other tubers used.

The total loss in 14 months amounted to 192 g. or but 13 per cent. of the original weight, although many branches and small leaves were produced in the summer of 1910. (See left-hand figure in Pl. X.)

Ibervillea No. 5 weighed 1·006 kg. on March 17, 1910. The rate of loss during the following days was but 3·6 g., which was probably less than that of No. 4, largely by reason of the small amount of damaged surface. The rate fell to 0·9 g. in April, and to 0·5 g. in early May. The rising temperatures failed to accelerate the loss, but the rate rose only when green stems were formed. These brought the loss to 0·6 g. later in May, 0·9 g. in June, and to 1·5 g. with the fullest development of the leafy stems in July. The gradual death of the stems brought the rate down to 1 g. daily in the 68 days ending October 3, 1910, 0·9 g. in November, and to 0·15 g. daily in the 91 days ending February 3, 1911. This minimum was equivalent to one part in over 5,000, which was much in excess of the loss displayed by No. 4. The excessive loss is to be attributed to the greater development of green stems, five of which remained alive. The room was warmed to 18° C. for a few hours every day in February, but the rate of loss rose to only 0·16 g. daily. The rate was 0·2 g. daily during the first 20 days of March, 0·2 g. daily during the next 60 days, and 0·32 g. daily in the period of 25 days ending May 1, when a number of rapidly elongating stems were being formed. (See lowermost figure in Pl. X.)

TUMAMOCA.

Tumamoca is a relative of *Ibervillea*, native to the region about the Desert Laboratory, and having similar habits. The tuberous formations which retain the balance of food-material and water, however, are formed underneath the surface of the soil, and the outer layers are not so impervious to water. One of these structures taken from the soil and cleaned, November 2, 1910, weighed 125 g. Upon being placed on a suitable support in the laboratory it lost 1·3 g. daily during the first two days, or one part in 93, although care was taken not to damage the outer layers. This high rate continued, being 1·37 g. during the next five days, although it fell to 0·3 g. daily during the 86 days ending February 3, 1911. Its net weight at this time was but 90 g. and the minimum loss was one part in 400, which is greatly in excess of that of its relative *Ibervillea*, under the same conditions. (See uppermost figure in Pl. X.)

The total loss from this plant amounted to 258 g. or about 25·5 per cent. of the original weight, which was greater than that shown by any other plant of this species. The excess is probably attributable to the greater number of green stems formed.

GROWTH ACTIVITIES OF DESICCATING PLANTS.

In addition to the observations made on the growth or quiescence of plants with a water-balance during a period of depletion recorded in the preceding pages, the unpublished results of a study of the formation of stems from desiccating tubers of *Dioscorea alata*, which were made in the New York Botanical Garden, by the author in 1902, are of interest in connexion with the subject under discussion.

Mature tubers produced by vines in the conservatories were placed in shallow glass dishes on tables within two or three metres from large windows in January of that year. The illumination did not differ greatly in intensity from that of the glass houses. Growth soon began and two or three buds awakened on each tuber, and the stems produced extended at an extremely slow rate during the following 20 months, with the result that an extension of 10 to 15 cm. was reached (Pl. IX, C). A comparative examination was made of this material with stems of vines in the conservatories and of the young stems sent out by tubers in the propagating houses. The work of Duchartre upon *D. Batatas*, Dcsne., was found of great interest in connexion.[1] Duchartre placed tubercles in a dry chamber where they would be compelled to sprout without a supply of soil moisture, in a manner similar to that noted above. He noted that the stems developed were 50 to 80 cm. long, composed of elongated internodes, and that the leaves remained extremely small with diminutive laminae, entirely lacking from lower internodes, and showed a lack of mechanical tissues, from which he points out the resemblances to etiolation as exhibited by some plants. The bases of the stems remained green, but the remainder of the epidermal structures were of a reddish brown colour. He also noted that the base of the stem became the seat of the formation of a tuberous swelling which must have been the beginning of the large tuber usually formed by these plants underground. No stomata were found on the reduced leaves, the starch was not all converted, and the unequal thickenings were not seen in the layer of cells usually becoming collenchymatous. (See Pl. IX, A and B.)

Miss Dale performed similar cultural experiments with *Dioscorea sativa*, although no reference is made by her to the previous experiments of Duchartre.[2]

In this case also elongated stems were formed which measured as much as six or eight feet. The formation of buds at the bases of the stems was noted, but no comparisons of the lengths of internodes with those of the normal were made. Tuberous structures were seen to develop in the axils of the leaves, and the branches remained very short. The formation of adventitious roots around the bases of the stems, with a scaly epidermis, was noted.

The stems in my cultures of *D. alata* did not seem capable of reaching the lengths described by Duchartre and by Dale in the two species named, but this deficiency may be accounted for in part by the smallness of the tubers and correspondingly small supply of food-material available. The stems consisted of two to five internodes, and were angular, reddish brown, and bore numbers of trichomes and glandular structures. The internodes were of a length less than that of the normal in every instance. The bases of the stems underwent a tuberous swelling from which arose numbers of short thick adventitious roots (Pl. IX, C).

The leaves were extremely small, and were in the form of narrow reddish brown scales, with no differentiation into lamina and petiole. The axillary buds showed an activity similar to that of the main buds of the

[1] Duchartre, P. : Influence de la sécheresse sur la végétation et la structure de l'igname de Chine *Dioscorea Batatas*, Dcsne. Bull. Soc. Bot. de France, vol. xxxii, 1885, p. 156.

[2] Dale, E. : On the Origin, Development, and Morphological Nature of the Aerial Tubers in *Dioscorea sativa*, Linn. Ann. of Bot., vol. xv, 1901, p. 491.

tubers, and the bases of the primary branches were expanded into tuberous formations in the same manner as the primary stems, but the adventitious roots formed did not progress beyond the form of papillate outgrowths. In no instance did the branches attain a length beyond a centimetre.

An examination of my material showed that the xerophilous stems had attained a degree of differentiation of the tissues much less than the normal, which may be attributed directly to the lack of formative material, including water. The pericycle might not be distinguished, and the cortical tissue was composed of cells of greater angularity of outline. Despite the lack of development in the stelar elements, the sub-epidermal parenchymatous elements showed marked collenchymatous thickenings, not seen in normal stems, while the outer walls of the epidermis were much heavier and were distinctly cutinized. (See Pl. IX, A and B.) It is thus to be seen that, despite the lack of nutritive material and the capacity for photosynthesis, the small resources of the shoot were directed towards the formation of elements which would operate to husband the minute supply of water and diminish transpiration. The differences in structural reaction in *D. Batatas* and *D. alata* may be accounted for chiefly by the fact that the tuberous formations of the first are thickened roots, while those of *D. alata* are undoubtedly stem structures.

General Discussion.

The vegetation of almost all desert regions usually includes a number of rapidly maturing forms, indigenous or of ancient or recent introduction, which carry out their entire cycle of existence during regular or irregular periods of rainfall, and are physiologically mesophytes. Other forms that require much moisture are to be found along streamways.

The specialized forms not affected by the streamways and more or less active during the dry seasons comprise two types, viz. the sclerophyllous and the succulent. The first includes a large number of woody and spinose herbs and shrubs with reduced branches, restricted spread of leaves, and indurated surfaces. These xerophytes have a very small water-balance, and the cell-sap may show extreme concentration. Determinations of the osmotic pressure of the sap of a number of such types at Biskra,[1] in Africa, by Fitting, gave pressures of 100 atmospheres and over. The roots of such plants are usually in continuous absorptive contact with soil particles from which some moisture may be withdrawn, and sclerophyllous forms are notably difficult to transplant, since they wilt so quickly when removed from the soil. Mesophytic plants, when grown under arid conditions, simulate sclerophylls to some extent, although the extremes of osmotic pressure of the sap are probably not approximated.

[1] See Fitting, H.: Die Wasserversorgung und die osmotischen Druckverhältnisse der Wüstenpflanzen. Zeitschr. f. Botan., vol. iii, 1911, p. 209.

Morphogenic reactions of a xerophytic character are well illustrated by the structural features of *Dioscorea* described in this paper.

The specializations exhibited by sclerophyllous forms are therefore of a direct physiological character and entail the least morphological change. This group is represented in American deserts by a large number of leguminous trees and shrubs, such as *Prosopis*, *Acacia*, *Calliandra*, *Parkinsonia*, *Cercidium*, *Olneya*, &c., and by *Covillea* (*Larrea*), *Fouquieria*, *Lycium*, *Koehberlinia*, *Condalia*, *Zizyphys*, *Manzanita*, *Quercus*, *Aster*, *Encelia*, *Franseria*, *Jatropha*, *Sapindus*, *Vauquelinia*, &c.

Succulents display most of the external features of the spinose xerophytes, which may be carried to their extremest limits. This is well exemplified by the Cacti, in which the entire shoot may be reduced to a short cylindrical or globose form. In addition to these reductions secondary morphological changes have ensued, which have resulted in exaggeration of the medullary or cortical tissues in roots, stems, or leaves, which may contain large balances of water. The sap of succulents generally shows a comparatively low osmotic pressure. Three to five atmospheres are usually found in *Echinocactus Wislizeni* when turgid. *Carnegiea* shows 6–8 atmospheres, and *Opuntia* 10–12; *Agave* slightly more; and the pressure in all of these may increase greatly with desiccation. The greater number of succulents in South-Western America are to be found in the regions in which the rainfall occurs regularly within well-defined seasons. This is true of the plants used in the experimental work described in the preceding pages. The root-systems of such plants are generally horizontally disposed within a few centimetres of the surface, and are in a position where the moisture is most available during the rainy seasons. The cessation of the rains is soon followed by a low water-content of the surface layers of the soil, and the passage of water from the soil to the plant is reduced to a minimum. The finer rootlets perish, and the plant stands self-contained until the next rainy season, when new absorbing branches are formed.

The actual physiological value of large water-balances varies widely, as may be seen by an examination of the experimental data given in this paper. The great Tree Cactus, or Sahuaro (*Carnegiea gigantea*), may survive a year or perhaps two, under certain circumstances, without receiving additional water from the soil. The formation of flowers in the arid fore-summer, however, will not take place unless the plant has received its supply during the previous winter rainy season. Neither would apical growth ensue in midsummer unless the summer rains were available. The death of a plant from the base upwards may sometimes result in the development of flowers on isolated branches which have received no water for a year, but this must be taken as a special case in accord with many experiences that approaching death stimulates reproduction.

Echinocactus was seen to exhibit both root development and apical growth of the stem after one or two years of depletion of the water-balance, and showed some capacity also for flower formation. Individuals exposed to the full intensity of the Arizona sunlight might not survive for more than a year, although even the slightest amount of shade would greatly enhance the value of the enormous water-balance. Plants in an ordinary room were in good condition after three years of deprivation of water.

Repeated observations show that the flattened Opuntias may exist for extended periods, perhaps two or three years, without a water-supply, and may carry out seed-formation during this period. New joints may be formed, but generally at the expense of the older ones, which are destroyed during the process.

Ibervillea has a great balance of food material as well as water, which is accumulated in woody tubers with heavily indurated outer tissues. These plants have been seen to be capable of developing the thin shoots for many years with a small rate of depletion. One individual has been under continuous observation for ten consecutive seasons. The intensity of the illumination and temperature, of course, figure largely in the matter.

The corms of *Brodiaea* respond to seasonal stimuli by the development of smaller new and turgid corms in prolonged periods of desiccation. The older corms are emptied and destroyed in the process, which may be repeated a few times.

No notable morphogenic departures were seen in the phenomena of growth and reproduction as exhibited by *Echinocactus*, *Opuntia*, and *Ibervillea* with a depleted water-balance, except that the new structures were generally of a minimum size. The stems of *Dioscorea* developed under such conditions, however, showed some notable departures towards a sclerophyllous habit. (See pp. 83–5.)

All of the plants examined showed a high rate of water loss immediately upon removal from the soil, due to evaporation from moist outer surfaces and from abraded tissues, regardless of the season. Next it was found that the curve of transpiration was lowest in the cool months of November, December, and January. At this time the daily rate of *Echinocactus* was between one in 40,000 of the total weight and one in 8,000 in a well lighted room, while individuals in the open showed a rate of one part in 5,000 to one part in 2,500, and even one part in 300 in a single instance. The maximum rate during the hot, dry fore-summer with relative humidities between 6 and 20 per cent. and midday temperatures as high as 90° F. indoors and 112° F. in the open, varied between one in 800 and one in 4,000 in a well lighted room, while it rose to one part in 300 for the entire period of February to May, and must have been double this rate in May.

The minimum daily rate of loss in *Carnegiea* (adults) was about one part in 9,000 of the total weight in a shaded room in winter, and the maximum in the open was one part in 640 after the plant had suffered several months' depletion. Seedlings of this plant lifted from the soil in November lost weight at the rate of one part in 12 daily for three days, the average during the next nine days being one in 40, which then rose to one part in 30 in midwinter, and fell later to one part in 227 in the period when some of the individuals were dying. This expected high rate of loss by desiccation would contribute to the enormous mortality of seedlings in the open. Germination takes place in the summer rains in July, and the tender plantlets must then endure a period of four months of extreme aridity, but with falling temperatures.

The resting corms of *Brodiaea* lost one part in 11 by evaporation from the dead outer coats the first day after removal from the soil in November, and this rate fell at once to one in 53, then to one part in 164, and finally to one part in 200. The latter rate was calculated for the period including the formation of new corms. This rate of loss is probably greater than that which would be exhibited by corms *in situ* in the soil.

The minimum rate of loss of *Ibervillea* during the relatively humid cool winter season was one part in 4,500 to one part in 32,000. The maximum in a well lighted room during the arid fore-summer was one part in 573 to one part in 2,000. This applies to the period in which new stems were being formed.

The behaviour of a plant in successive seasons with especial relation to the state of depletion of its water-balance of succulency was a matter which received some attention. *Echinocactus* No. 1 showed a maximum rate of 29 g. daily in 1908, and 15·6 g. a year later, after it had lost but 3 kg. or 7 per cent. of its weight. The minimum rate in March, 1908, was 10 g. daily, while a year later, in the corresponding season, it was less than 4 g. after a loss of but 3 kg. or about 7 per cent. of its weight.

Echinocactus No. 6 lost at the rate of 0·6 g. daily during 155 days including the winter of 1908–9, and 3·7 g. daily during a corresponding period of 173 days a year later, after it had decreased 1·370 kg. or 3·8 per cent. of its earlier weight. A year later the rate was 2·8 g. for a period of 188 days after a loss of but 1·600 kg. more. The maximum rate in June, 1909, was 10 g. daily, and in June and July, 1910, 7 and 7·7 g. daily, after a loss of 1·865 kg. or less than 7 per cent. of its total weight. *Echinocactus* No. 7 lost 9 g. daily in 56 days in midwinter of 1908–9, while the rate was 2·3 g. daily for 109 days in the corresponding period of 1909 and 1910, after a loss of 2·653 kg. or 7·5 per cent. of the earlier weight.

The above data were taken from plants kept in the laboratory, in which corresponding seasons would be fairly equalized.

Echinocactus No. 13 lost at the rate of 150 g. daily during 83 days ending May 12, 1910, and 10 g. daily in the 42 days ending March 20, 1911, after its weight had decreased nearly 50 per cent. This plant was exposed in the open.

An *Ibervillea* tuber lost at the rate of 0·8 g. in May, 1910, and at the rate of but 0·12 g. daily in May, 1911, after the weight had decreased 15 per cent. Green stems were present, and the conditions fairly equivalent in the two periods.

Ibervillea No. 4 lost at the rate of 0·8 g. daily in 15 days ending May 26, 1910, during which time new stems were starting, and at the rate of 0·16 g. daily under equivalent conditions in 1911, after the weight had decreased 15 per cent.

Ibervillea No. 5 lost at the rate of nearly 0·7 g. daily in 15 days ending May 26, 1911, under equivalent conditions, after the weight had decreased 22 per cent.

The green stems were especially vigorous in No. 5, and to their activity must be attributed the excessive total and high rate shown in May, 1911. An inspection of these data shows that a total loss of 15 per cent. in weight was followed by a decrease of 85 per cent. in the rate, a loss of 8 per cent. in weight by a decrease of 80 per cent. in the rate, a loss of 22 per cent. in weight by a decrease of 56 per cent. in the rate, in tubers of *Ibervillea*. The significance of these measurements is partly obscured by the activity of newly developing green stems, but it is evident that the major variation in the transpiratory loss with progressive depletion of the water-balance (which in turgid individuals would be 60–80 per cent. of the total weight) is not to be attributed to climatic variation, or the activities of stems formed, although the influence of the last-named feature is obvious.

The evidence furnished by the individuals of *Echinocactus* free from the influence of factors which would prevent a fair comparison affords some further illustration of the matter.

Echinocactus No. 1 lost water at the rate of 109 g. daily in March, 1908, and at the rate of 3–5 g. daily in March, 1909, a decrease of 50–66 per cent. in rate with a lessening of the water-balance of about 7·7 per cent. The maximum rate in May, 1908, was 29 g. daily, in June, 1909, 15·6 g. daily, a decrease of nearly 47 per cent. in rate with a loss of 7·2 per cent. in weight.

Echinocactus No. 4, which had already been exposed in the open for eight months, lost at the rate of nearly 0·45 g. daily in 182 days ending May 21, 1909. The loss during the 209 days ending May 13, 1910, was at the rate of about 0·24 g. daily, a decrease of nearly 50 per cent. in rate after a total decrease of about 7 per cent. of the earlier weight.

Echinocactus No. 6 lost at the rate of 6 g. daily for 155 days ending May 12, 1909. In 177 days ending May 13, 1910, the rate was 3 g. daily, a decrease of 30 per cent., although the weight had fallen but 4·7 per cent.

The rate was but 2·3 g. in 157 days ending April 10, 1911, a decrease of 23 per cent. in the rate although the weight had fallen but 3·5 per cent.

Echinocactus No. 13 lost at the rate of 150·5 g. daily in 83 days ending May 12, 1910, and after a decrease of 28·6 per cent. of the remaining weight, the rate was less than 11 g. daily, a decrease of 92·6 per cent.

Five possible causes which might have influenced the rate of transpiration of a desiccating succulent present themselves. These are as follows: 1st, the increased concentration of the cell-sap, which was of such degree in the experiments as to increase osmotic pressures from 4 or 5 to 10 or 12 atmospheres, might retard evaporation from the cell-membranes; 2nd, a diminution of the degree of succulence, or proportion of water per unit area of surface present might lessen evaporation; 3rd, desiccation may result in alterations in the character of the outer membranes, or of any of the transpiring walls of the plant; 4th, desiccation may stimulate the formation of new tissues or the alteration of existing cells in such manner as to close openings through which water vapour might pass; and 5th, the positions of the surfaces might be shifted in such manner as to vary the exposure and lessen transpiration.

Livingston has recently pointed out that a concentration of the sap, even if carried to a point where an osmotic pressure of 100 atmospheres was exhibited, would not give a retardation of more than 10 per cent. from the rate afforded by a pure water surface.[1] It is evident, therefore, that this factor is negligible in the present discussion, as the increases found were not more than 5 or 6 atmospheres.

The records of the observations are not sufficiently complete to permit any accurate integration of the influence of succulence upon the rate of transpiration. The course of events in the behaviour of *Echinocactus* No. 13 shows a fair correspondence between the two in the course of rapid desiccation in the open air. The rate of loss diminishes so much more rapidly than the estimated degree of succulence in slowly desiccating individuals that it is impossible to escape the conclusion that other agencies are operative. Thus, *Echinocactus* No. 1, weighing over 42 kg. in March, 1908, may be safely estimated to have contained at least 92 per cent. or 39 kg. of water, and by comparison with No. 13 would have a relative succulence of 3 and a surface of 13,000 sq. cm. The rate of transpiration was 10 g. daily. A year later the degree of succulence after a loss of 3 kg. may be estimated at 2·76, with no allowance for diminished external area. The rate of loss, however, was 5 g. daily, a decrease of 50 per cent., although the succulence had fallen but 8 per cent. If an allowance were made for the shrinkage of external area, the disproportion would be greater, as the

[1] Livingston, B. E.: The Relation of Osmotic Pressure in Plants of Arid Habitats. Plant World, vol. xiv, 1911, p. 153.

actual decrease in succulence was probably not more than 5 per cent. Data from *Echinocactus* No. 6 for longer periods are equally interesting. This plant contained about 27 kg. of water December 8, 1908, and with a succulence of 3 would offer a surface of 9,000 sq. cm. The rate of loss for the 155 days ending May 12, 1909, was 6 g. daily. November 18, 1909, a further loss, 2·335 kg., had ensued and the succulence was then 2·7 daily. In the 178 days to May 13, 1910, the rate of loss was but 2·8 g. daily. The succulence had decreased 10 per cent. and the transpiration rate 53 per cent. The annual growth and consequent accelerated loss in *Ibervillea* makes the data from these plants ineligible in the present connexion.

The approximation of the ridges or folds in *Echinocactus* would operate to diminish the angle of exposure to the sun and the consequent transpiratory loss. A detailed examination of *Echinocactus* has not been made, but the corky outer layer of the tubers of *Ibervillea* is being added to at intervals, and changes of this character would lessen the water loss.

The total losses from various plants in which the course of desiccation was not disturbed is given below :—

Name.	*Original weight.*	*Total loss.*	*Proportion.*	*Period.*	*Remarks.*
Echinocactus.					
,, No. 1.	42·743 kg.	4·583 kg.	11%	15 mo.	In shaded room. Died.
,, No. 2.	5·136 kg.	1·724 kg.	33%	18 mo.	Shade and open air. Living.
,, No. 4.	1·192 kg.	0·643 kg.	54%	36 mo.	Died.
,, No. 6.	28·573 kg.	3·713 kg.	13%	30 mo.	Shade. Living.
,, No. 7.	35·818 kg.	4·248 kg.	11%	30 mo.	Shade. Living.
,, No. 13.	49·390 kg.	23·850 kg.	48%	13 mo.	Open. Living.
Carnegiea.					
,, No. 1.	40·000 kg.	11·250 kg.	28%	12 mo.	Open air and shade. Living.
,, No. 1*a*.	45·325 kg.	10·535 kg.	23%	16 mo.	Open air. Living.
20 seedlings.	27·244 g.	17·745 g.	54·7%	102 da.	Shade. 4 dead.
Brodiaea.					
36 resting corms.	46·700 g.	18·425 g.	39·5%	96 da.	Shade. Young corms formed.
Ibervillea.					
,, No. 0.	530· g.	143· g.	27%	19 mo.	Shade. Sending up shoots annually.
,, No. 4.	1·452 kg.	164· g.	11·5%	14 mo.	Shade. Annual shoots.
,, No. 5.	1·006 kg.	278· g.	27%	14 mo.	Shade. Annual shoots.
Tumamoca.					
Tuber	125· g.	34·4 g.	17·5%	4 mo.	Shade. Died.

No special attention was given to the matter of absorption of water or water vapour by the plants which were used in the experimental work. The results of the weighings, however, disclose the fact that small individuals of *Echinocactus* made a net increase in weight when placed in a dark room with a relative humidity of 80–90 per cent., after removal from a room with a humidity of 15–30 per cent. Other specimens made similar gains when brought into a shaded room from the open air. Still another specimen showed a distinct gain in the open during a night of drizzling rain. As these plants are provided with a dense armature of long curved spines (see Pl. VII) which are hygroscopic, their dead tissues dry out under arid conditions and appear to take up water or aqueous vapour, as any bit of dry wood might do it. The bases of these spines are made up of heavy-walled tissues through which water might pass with difficulty. It is probable, therefore, that the changes in weight of *Echinocactus* due directly to humidity do not affect the succulence of the living tissues, and concern the dead spines only.

The actual behaviour of the spines with regard to atmospheric moisture was tested in July, 1911. The spines from two ridges of a plant 50 cm. in height were detached and sent to the acclimatization laboratory at Carmel, California. The lot was placed upon a suitable sheet of paraffin paper and found to weigh exactly 20 g., in a sunny place, at noon on July 8. After exposure to the humid air in the open throughout the night, the weight was found to be 20·400 g. at 9.15 a.m. on the 9th, after some drying out had taken place. Desiccation occurred as before and the spines were again placed in the open and sheltered from precipitation, at 7 p.m. on the 10th. The night was foggy and misty and the spines absorbed so much that the weight had increased to 20·745 g. at 7 a.m. on the 11th. The lot of spines was practically equivalent to those clothing *Echinocactus* No. 4, and was about one-tenth of the whole number on the plant from which they were taken. The total weight variation on such a plant due to imbibition and desiccation of the spines might, therefore, be about 7 or 8 g. daily, and on the largest individuals two or three times this amount. The proportion of weight variation due to such causes would be large in small plants.

The conditions presented are different from those studied by Spalding,[1] Schönland,[2] and Marloth. Marloth[3] detected positive absorption of water and water vapour by the hairs of *Mesembryanthemum* and *Crassula*, and the structure of one type of trichome in the younger stage is such as to permit the passage of water into the living cells. Lloyd found that water absorbed by the loose bark of *Fouquieria* passed into the living tissues, and that the consequent increase of the water-balance was followed by the unfolding of new leaves in stems, quiescent at the beginning of the experiment.[4] Miss Delf demonstrated that water in liquid form as well as a vapour might pass the epidermis of the green parts of *Suaeda maritima* and *Sali-*

[1] Absorption of Atmospheric Moisture by Desert Shrubs. Bull. Torr. Bot. Club, vol. xxvi. 1906, p. 367.

[2] On the Absorption of Water by the Aerial Organs of some Succulents. Trans. Roy. Soc. South Africa, vol. i, part II, 1910, p. 395.

[3] Notes on the Absorption of Water by Aerial Organs of Plants. Trans. Roy. Soc. South Africa, vol. i, part II, 1910, p. 28.

[4] The Artificial Induction of Leaf-formation in the *Ocotillo*. Torreya, vol. v, 1905, p. 175.

cornia annua, when the water-balance was low, and that absorption through immersed surfaces was exhibited by many plants.[1]

Purpose and adaptation may be easily read into such action. This kind of an interpretation seems forced, however, when it is considered that a capacity for absorption depends upon physical qualities, the primary significance of which relates wholly to other features of the activity of the plant.

EXPLANATION OF PLATES VI–X.

Illustrating Dr. MacDougal's paper on 'Water-balance'.

Plate VI. *Echinocactus Wislizeni*, normal and cristate specimen below. Two plants of *Carnegiea gigantea*, the taller of which is about 150 years old. The smaller plant has been girdled by rabbits, and may survive many years in this condition.

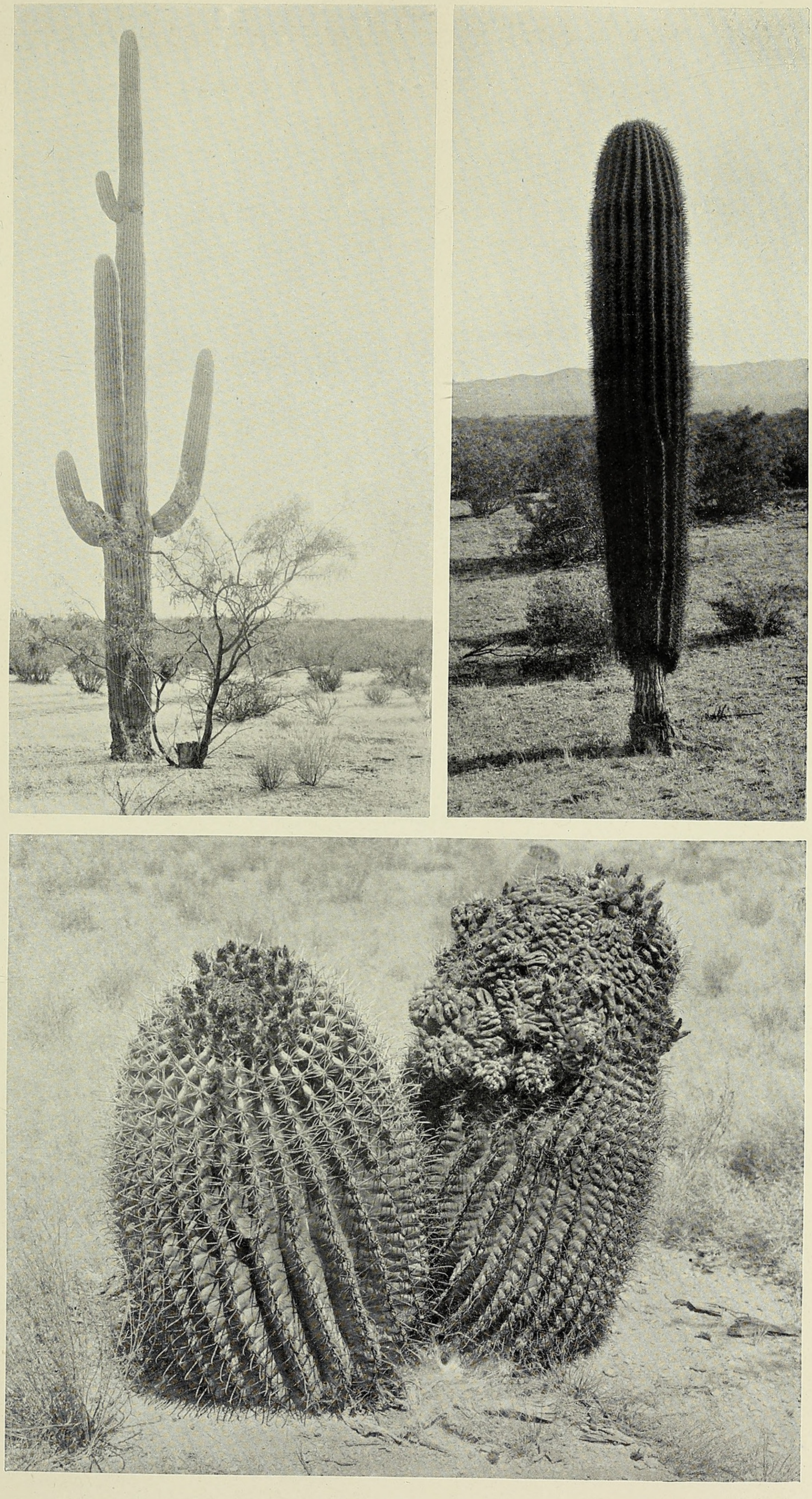
Plate VII. *Echinocactus* No. 4, with water-balance depleted by desiccation for 30 months.

Plate VIII. *Ibervillea sonorae*, with old stem climbing on branches of *Parkinsonia microphylla*.

Plate IX. A, Partial transverse section of stem of *Dioscorea alata* formed by desiccating tuber; B, from normal stem of same; C, tuber of *Dioscorea alata* with stems formed during desiccation. D, *Brodiaea*, with young corms formed during the desiccation.

Plate X. Tubers of *Ibervillea* and *Tumamoca* after desiccation for one year. Living and dead stems formed during this period are still attached.

[1] Transpiration and Behaviour of Stomata in Halophytes. Annals of Botany, vol. xxv, April, 1911, p. 485.



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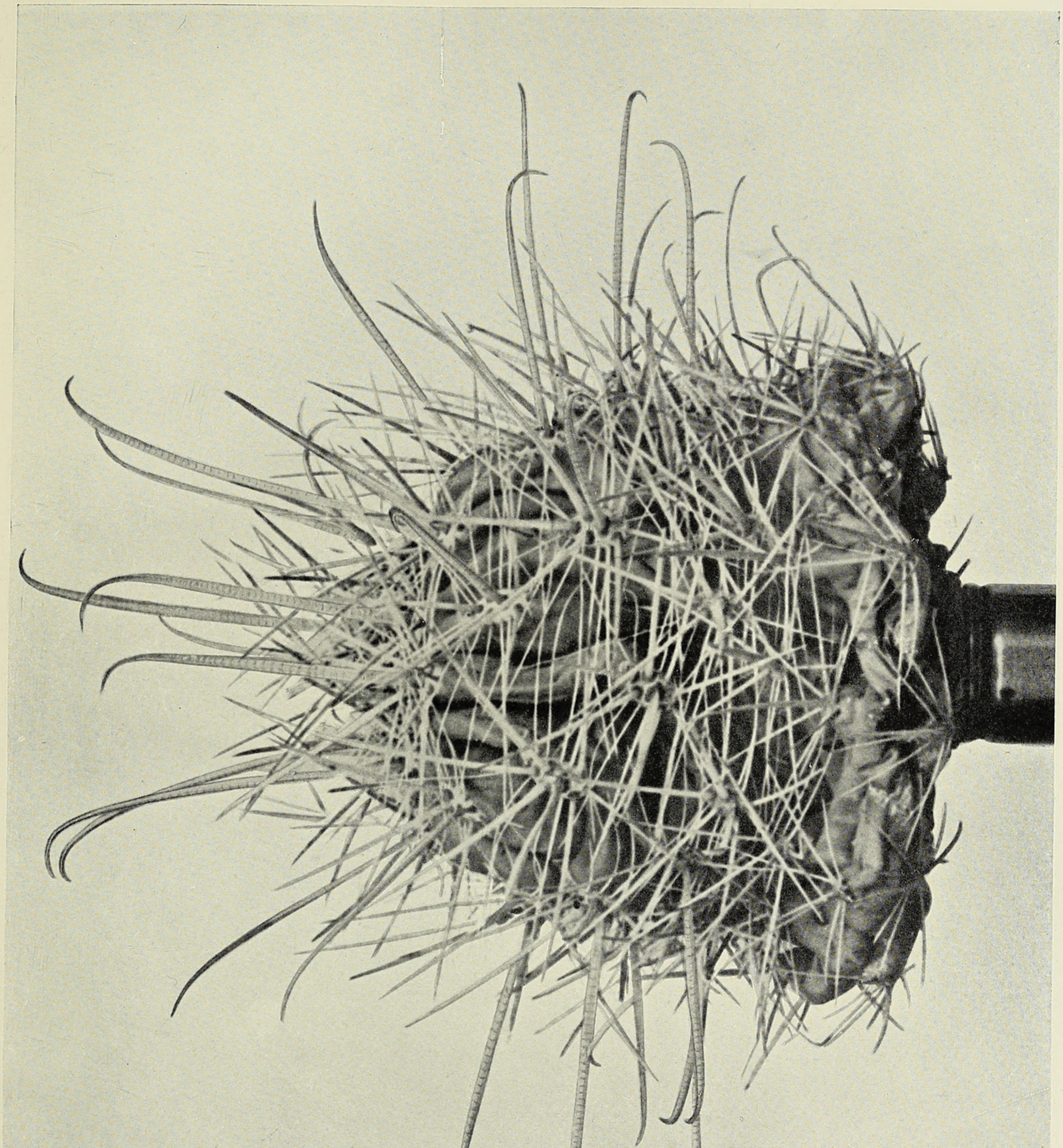

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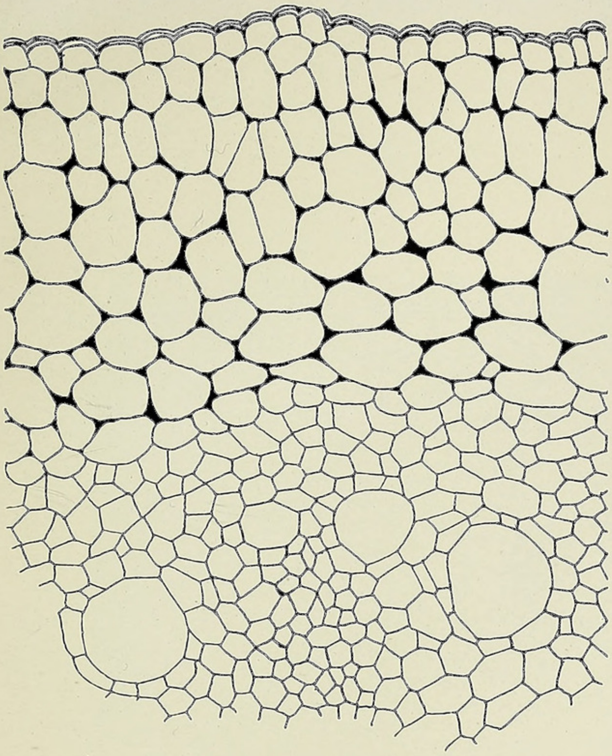

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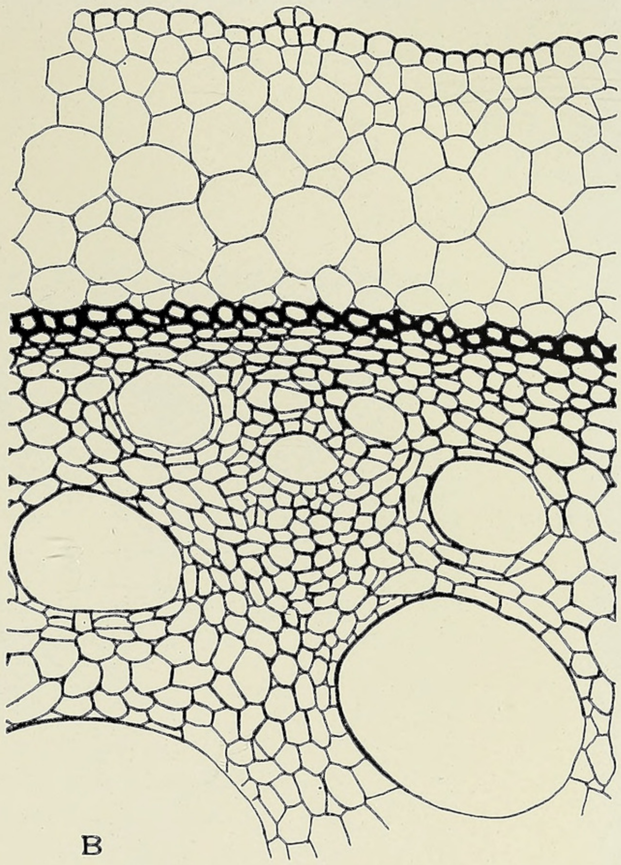

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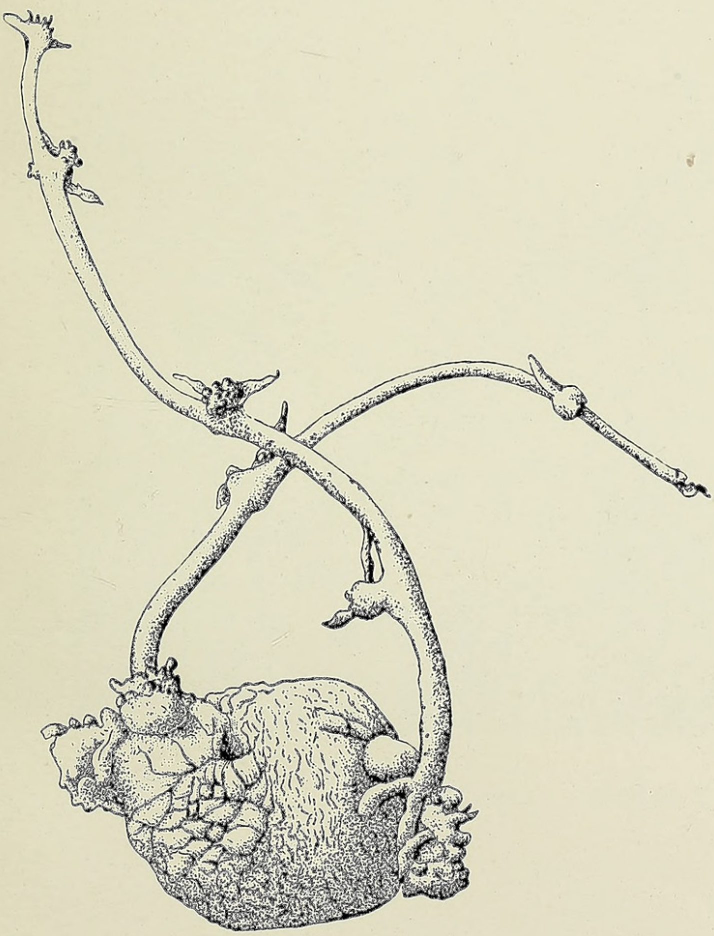

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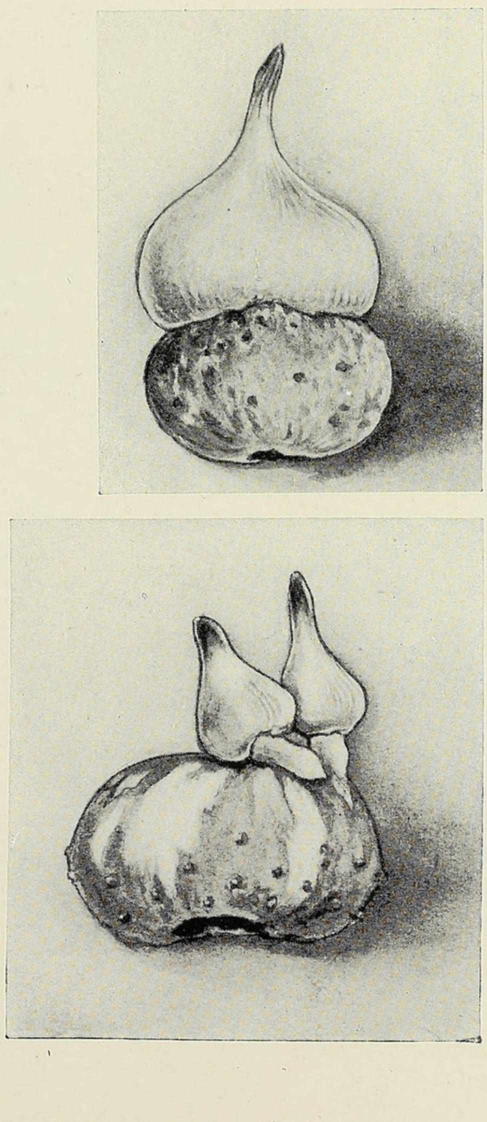

D

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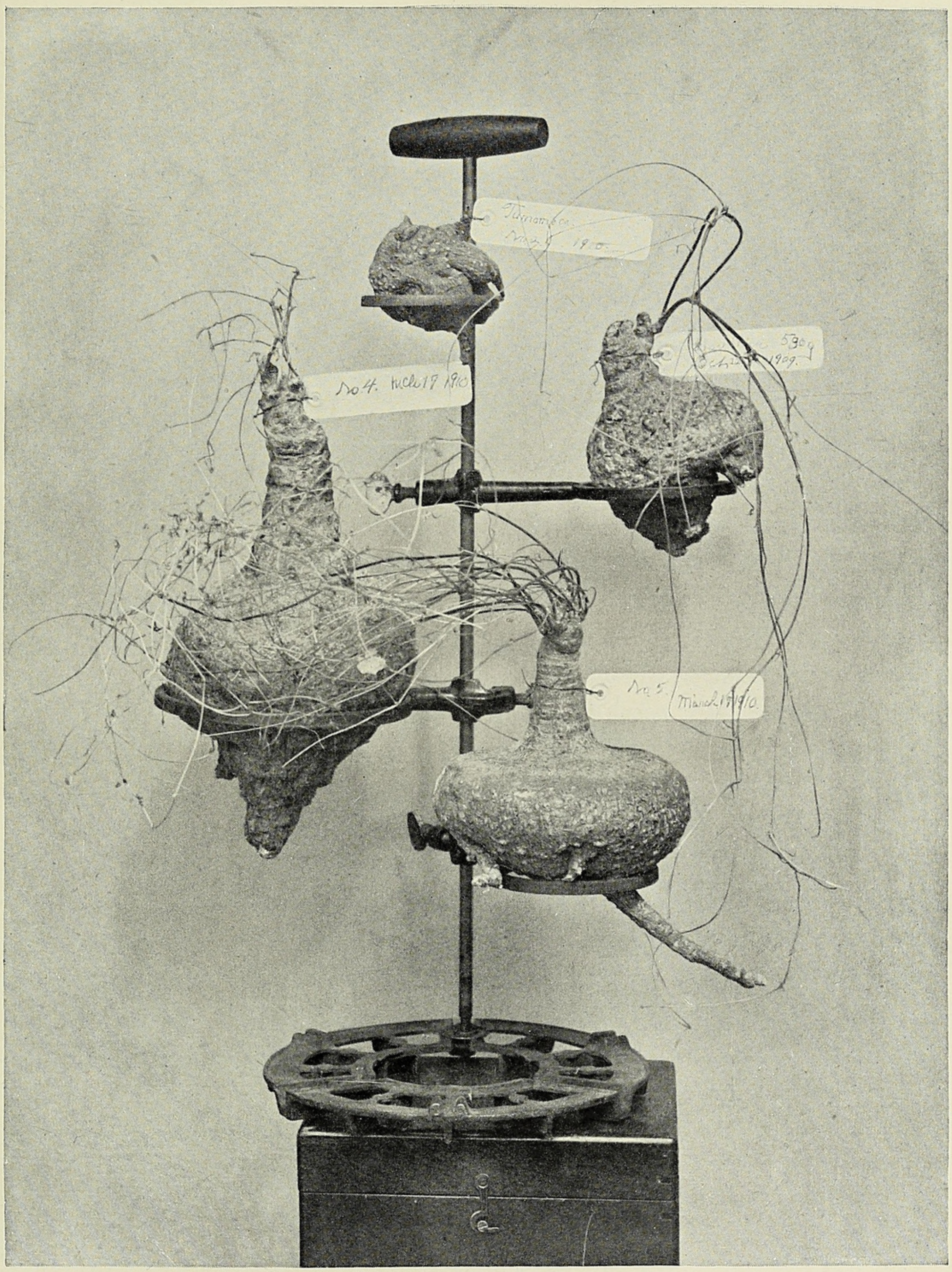

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