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ANNUAL REPORT OF THE DIRECTOR OF THE
DEPARTMENT OF BOTANICAL RESEARCH

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DEPARTMENT OF BOTANICAL RESEARCH.*

D. T. MACDOUGAL, DIRECTOR.

The activities of the year have been rewarded by definite progress in the study of all of the groups of problems under consideration. Some of the more important results may be briefly summarized as follows:

Growth in plants takes place at the expense of definite or formative compounds, which are formed locally at a rate determined primarily by the influence of temperature on chemical velocity. These constructive processes may be masked or checked by imperfect respiration, and enlargement depends upon conditions favorable to water-absorption. Light breaks down the smothering acids resulting from incomplete respiration in cacti and thus facilitates the construction of formative material. The lessened acidity resulting from the action of light is a condition of increased absorption of water, so that light may accelerate growth in two different ways.

Improvements in auxographic instruments and the designing of glass screens of specialized transmissibility of light have been accomplished.

The readily varying permeability of protoplasm is referred to the interrelations of the disperse-phase and disperse-medium of the hydrophile emulsion colloids of which it is made up.

Repetition of the experiments upon respiration with temperature controlled to within 0.02° C. demonstrates conclusively that sunlight causes changes in the air, as a result of which respiration (as measured by excretion of carbon dioxide) is highest on days of high solar radiation, less on cloudy days, and least at night. Arrangements are being made for measurements of the electrical conditions of the air under identical conditions.

In the study of the possible phases of photosynthesis in plants solutions of carbon dioxide and potassium carbonate have been reduced to formic acid by exposure to light from a mercury-vapor arc in a quartz tube. Next a sugar-like substance has been obtained by exposure of formic acid to sunlight and to ultra-violet light. This substance gives the reactions of sugar and can be used as food by green algae in darkness.

Succulent plants desiccated for long periods may show normal proportions of water-content, owing to the coincident respiration or oxidation of solid material.

The hydrolyzable carbohydrates of such plants starved for periods of one to six years were decreased, but the proportion of non-reducing sugars increased during starvation. Hydrolysis of cell-walls, deformation and peripheral thickening of the nuclei, and reduction of the

*Situated at Tucson, Arizona.

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4 Apr 33 Brown

protoplast were included in the starvation phenomena. Some starvation effects remain after several years of restored normal conditions.

The reduction of transpiration or water-loss in desert plants is not one of maximum rate, but consists in a check or lessening of the rate earlier in the day than in other plants.

The densities of the sap of desert plants are lowest in species native to arroyos and ascend in a scale through those of cañons, rocky slopes, and bajadas to the highest values in saline areas.

The successions of plants which occupy an area originally bare finally reach a climax formation the nature and permanence of which are determined by climatic control. Four great vegetation eras, viz, Eophytic, Palæophytic, Mesophytic, and Cenophytic, can be recognized in the history of terrestrial vegetation.

The chief physical factors and their determinative effect upon vegetation at various altitudes from a low desert to the top of an insular mountain have been evaluated.

The field work necessary to a complete survey of the Cactaceæ has been brought to an advanced stage by expeditions to the West Indies, Brazil, and Argentina.

The Salton Sea receded about 50 inches during the year ending July 1, 1915, an amount in excess of that of the previous year. The total recession now amounts to nearly 40 feet or nearly one-half the original maximum depth. The total dissolved salts has increased from 0.32 per cent in 1907 to 1.37 per cent in 1915. The heightened salinity of the water has been followed by changes in the revegetation of the beaches and by the cessation of deposition of calcium carbonate on fixed objects near the surface. This implies changes in the marine as well as in strand organisms.

Preliminary examination of the playas, bajadas, streamways, lake beds, faults, and terraces of the Mohave Desert region has disclosed evidences of climatic variation and of movements of the surface which it is hoped may be interpreted to account for the origination, phylogeny, and successions of the vegetation which now characterize the region.

The desert rubber plant (*Parthenium argentatum*) under domestication has been found to show over 100 strains separable by habit, structure, form, and rubber content.

The studies of the rôle of the factors in a desert complex prove that the more divergent part of a population is eliminated by environic agencies, but this eliminating action is subject to various modifications.

The mutating stocks of beetles have continued to produce mutants as in previous years, one being an additional or second departure from the original. Another type of modification, consisting in alterations of the stripes on the elytra of beetles, which was first apparent as a small variation or departure, shows an orthogenetic progression, the new characters being genetically stable.

The year has been characterized by the most cordial cooperation on the part of a number of institutions, some of which have borne a share of the expense of researches carried on at the departmental laboratories, and cash donations to defray the expense of certain researches have been received.

EQUIPMENT.

The cages for testing environic effects on plants and beetles having become unsafe and unsuitable, a new suite was constructed, with bases of brick and cement and tops of cypress suitable for holding netting or glass, and temperature-control apparatus has been installed in several experimental units. The most notable addition to the equipment consisted of the new laboratory for phytochemical research.

The investigations of the last four years on the relation of light to organisms have clearly revealed the fact that the most hopeful point of attack of these highly complex problems is the study of the chemical changes produced by light. Such a study naturally requires chemical and physico-chemical investigations of a highly specialized nature. In accordance with these requirements a new laboratory was designed for the study of the chemical and physiological effects of light, and this was completed in November 1914.

The building, 50 by 28 feet, is of stone; the inner walls are pressed brick. It contains two laboratories equipped with water, gas, direct-current and alternating-current electricity, vacuum, air-pressure, and large fume hoods. There are also a small shop and preparation room, a machine room for vacuum and pressure pump, 4-horsepower motor generator set, water-still, etc., a study, and a capacious attic used for storage and in connection with experiments on the roof. One side of the main laboratory, 23 by 25 feet, is arranged and fully equipped for chemical work; the other side is devoted to work with plants, microscopic-work table, and the thermostatic apparatus for the investigations of the effect of sunlight on respiration. The other laboratory is a photo-chemical dark-room for work with artificial sources of light as well as sunlight, spectroscope and polariscope work, etc. On the roof there is an insolation deck, 30 by 15 feet, covered with sheet lead; this is virtually an open laboratory affording excellent facilities for special chemical and physiological experimentation with sunlight.

PHOTOLYSIS, RESPIRATION, HYDRATATION, AND GROWTH.

The Mechanism and Conditions of Growth, by D. T. MacDougal.

Auxographic records of the growth rates of seedlings of corn, wheat, and opuntia at the Desert and Coastal Laboratories include continuous tracings of the growth expansion of a large number of plants during the entire development of leaves and of segments of flattened stems.

Some individuals were followed without interruption for periods of 70 days under measured or controlled conditions.

The reduction and analysis of the data concerning growth in plants has made it possible to formulate some advanced general statements. The whole process of enlargement includes the synthesis, or solution of food material by hydrolysis of accumulated supplies, the conduction of solutions to the enlarging tracts and its conversion into the specialized formative material necessary for the growth of organs of all kinds. This is followed by the incorporation of the material in the plasmatic colloids and their derivative and accessory structures.

Photosynthesis (or other reduction processes), hydrolysis, and the final utilization of food-material in the construction of formative substances are chemical processes the velocity of which is so influenced by temperature as to be increased 2 to 7 times for every rise of 10° C. The delicate response of growth by changes in rate under variations of 1° to 2° C. support the inference that temperature is the dominant factor in controlling growth by its effect on the availability of the food-supply. This agency, of course, also affects the rate of conduction of food-material and of its introduction into growing masses, but in very much less degree than it exerts on chemical reaction.

The utilization of food-material, in which the carbohydrates are the most important constituent, includes some breaking down of the sugars, the initial changes being enzymotically induced, followed by oxidation of the waste or derivatives (organic acids) not actually used as building material. The rate at which the first stage of the process proceeds depends upon the removal of the acids, which not only check respiration, but also by their effect on the plasmatic colloids lessen the hydration capacity or swelling power of plasma and cell-walls. The acid wastes are disintegrated by the action of light, with a resultant acceleration of respiration and of the construction of "formative material." The capacity of the growing parts to take up water is increased coincidentally.

The above effects are well exemplified by the behavior of growing joints of *opuntia*, of which several hundred records are available. The daily history of a growing joint includes an acceleration in the forenoon, during which time the acid wastes are being broken down by light, the maximum rate of growth being reached after noon with the consumption of the accumulated food-material. The elongation slackens or proceeds according to the diminished supply, and with the coming of darkness may actually cease by the hemming action of accumulated acids. Actual shortening may ensue during the night because of decreased hydration capacity resulting from low temperature and acidulation. The dawn brings the disintegrating effect of light on acids and the resumption of growth.

Light of the shorter wave-lengths (blue-violet rays) has a further possible effect on growth in that it coagulates or neutralizes colloids (suspensoids) and reduces their hydratation capacity, and may also possibly break down some nuclear substances. The radiation in question, however, has the least penetrating power of any part of the spectrum, and hence its action is most marked in minute organisms, or those with translucent membranes. Marked morphogenic alterations in the higher plants may be induced by illumination from a mercury-vapor arc in a quartz tube.

Methods and Material for Study of Fundamental Processes of Growth,
by D. T. MacDougal.

Nearly all available data concerning growth of the higher plants have been obtained by a study of single organs of seedlings, measurements being made under conditions not capable of yielding conclusions of wide application, or which afford a basis of analysis of the contributory processes.

An inspection of the material available at the Desert Laboratory made it apparent that the flattened opuntias offered certain structural features and habits of growth which promised unexcelled opportunities for analyses of some of the physico-chemical processes of growth and to make exact measurements subject to well-defined corrections. The joints of these plants emerge as small flattened buds, thickly covered with ephemeral leaves, and they expand to a length of 15 to 20 cm. and a width of 8 to 16 cm. in about two months.

The growing joints are firm enough to give steady contacts with counter-weighted levers carrying a pen which traces the expansion or other change in volume continuously. The joints are complex as to morphogeny, but enlarge as simple but heterogeneous disks of plasmatic colloid against distensible membranes and fibro-vascular skeletons. The transpiration, stomatal action, respiration, and the major features of sugar content and acidity of these plants are known, so that it was possible to connect alterations in rate of growth with chemical conditions in the joint, a connection not hitherto adequately established. Instead of a single series of chambers with temperature control, it has been found most effective to establish separate small chambers at the various small experimental plants. Light screens of various transmissibility as described in the previous section have also been devised and constructed. The compound-lever systems used to obtain the auxographs of some of these plants were adjusted to record all variations in the dimension being measured. The slackened elongation rate and the shrinkages detected in the tracings, which in some cases extended for ten weeks without break, furnished evidence upon which important contributions may be made as to the relation of acidity and respiration to growth.

Influence of Light upon Growth and Development, by D. T. MacDougal.

The author began work on this subject in 1899 and completed an extensive study of the growth and development of plants in darkness in 1903. The conclusions reached at that time included a generalization to the effect that light does not exert an invariable effect on the rate of growth. The completion of studies of Richards and Spoehr at the Desert Laboratory, upon respiration and acidity, have now yielded some new views and gained some vantage-ground for a new attack upon the subject.

The organization of this work has required the testing of suitable sources of light and the construction of a suite of plane and parabolic silvered mirrors by Dr. Ritchey, of the Solar Observatory. The greatest technical difficulty that has been met and overcome, however, has been that of securing screens of glass by which light of certain wave-lengths only might be thrown on the experimental objects. A number of these have been obtained by the cooperation of Dr. H. P. Gage, of the Corning Glass Works, and as soon as testing facilities are organized these screens will be made available to other laboratories. Satisfactory formulæ have been found for a good monochrome red which removes all light of wave-length shorter than 0.61μ with a refractive index of 1.507; a yellow-red transmitting red-yellow and green to 0.53μ ; a blue transmitting the blue violet from 0.52μ , and hence being complementary to the last; "uviol" transmitting the entire visible spectrum, and a "heat-absorbing glass" which absorbs the infra-red. The last-named has some promise of utility in glazing windows in warm countries.

The preliminary tests give some indication that the influence of illumination is due to the combined effect of wave-length, total energy, and relation to the absorption spectrum of chlorophyll. The most obvious results are of a morphogenic character, although the rate and amount of growth are doubtless affected.

*The Relation of Soil Aeration to Plant Growth, by E. E. Free and
B. E. Livingston.*

Experiments with *Coleus*, carried out in the Laboratory of Plant Physiology of the Johns Hopkins University, appear to indicate that this plant requires a certain low rate of oxygen supply to the soil in which it is rooted. The soil-moisture content in these experiments was kept near the physiological optimum and almost constant, by means of auto-irrigators, and a somewhat elaborate system of apparatus allowed the oxygen supply to the soil of the cultures to be cut off and renewed at will. Stems and foliage were exposed to the greenhouse air as usual.

The first noticeable effect of cutting off the supply of oxygen to the soil was a cessation of water-absorption by the roots, as indicated by the fact that the soil ceased to take water from the irrigators.¹ This indication

¹Livingston and Hawkins, Carnegie Inst. Wash. Pub. No. 204, 3-48, 1915.

was accompanied by cessation of growth and was soon followed by wilting. If wilting was not allowed to go too far the plants could be revived by renewing the access of oxygen to the soil. The injurious response was rapid and the revival slow. This study will be continued. It has a number of important relations to both theoretical and practical problems of the relations of plants to the soil solution.

Physiological Indices of Temperature Efficiency for Plant Growth,
by B. E. Livingston.

The interpretation of climatological temperature data with reference to plant growth has received still further attention during the past year. Livingston and Livingston¹ have summed the normal daily mean temperatures above 39° F. for a large number of stations in the United States, for the period of the average frostless season, and have also summed, for the same period, the normal daily chemical indices of temperature efficiency (supposing that chemical reactions double in velocity with each temperature rise of 18° F.). They show that the two charts of temperature efficiency values thus obtained, tentatively representing the temperature influence for the entire period of the average frostless season, are remarkably similar, but differ in certain important details. Neither of these two methods of temperature efficiency summation has any direct physiological basis, and it is obvious that neither method can be regarded as plausible for the higher temperatures observed in nature; for both methods proceed on the supposition that plant growth should continue indefinitely to increase as the temperature rises, and this is well known to be in disagreement with physiological observation.

The publication of Lehenbauer's study of the relation between temperature and the rate of growth of the shoots of maize seedlings² made possible a first attempt to derive physiological indices of temperature efficiency for plant growth. Lehenbauer's graph of observed growth-rates for shoots of maize seedlings, for 12-hour exposures to maintained temperatures, was conventionally smoothed, by means of a spline, and the ordinates of the smoothed graph were measured for each whole degree Fahrenheit. The values thus obtained were then expressed in terms of the value for 40° F., taken as unity, and these numbers are tentatively regarded as indices of temperature efficiency for plant growth. In making the summations for the climatological study, each day in the period of the average frostless season is represented by the efficiency index corresponding to its normal mean temperature and all of these indices for the period are summed for each station considered. This method of summation has a theoretical advantage over those heretofore tested, namely, that it takes account of the existence of the physiological temperature optimum; the table

¹Bot. Gaz., vol. 56, 349-375, 1913.

²Physiol. Res., vol. 1, 247-288, 1914.

of efficiency indices here employed indicates that the growth-rate is the same for a temperature of 40° as for one of 116° , and that it is about 122 times as great for a temperature of 89° as it is for one of 40° F.

A Simple Climatic Index, by B. E. Livingston.

Various studies heretofore reported, bearing on the relation of climatic conditions to plant growth, have been aimed toward the expression of all climatic influences, for any given station, by a single numerical value. While this aim is a sort of ideal abstraction that must long remain quite out of reach, it appears that progress enough has now been made toward the dynamic analysis of plant relations, so that a first tentative approximation may be proposed. The present proposal involves the use of the precipitation-evaporation ratio of Transeau (which may be taken as a roughly approximate index of the water-relations of plants, so far as these are determined by climatic conditions) and the summation of the daily physiological indices of temperature efficiency (which is similarly considered as a measure of the temperature condition). The precipitation-evaporation ratio is determined for the period of the average frostless season, and this value is multiplied by the temperature efficiency summation for the same period. The climatic product thus derived is proposed as an approximate index of the normal climatic efficiency for plant growth, for the station in question. This value may be derived for a large number of stations and a climatic chart may be constructed from the data thus obtained, and such a chart exhibits several fundamental features not shown by the charts of any of the simple climatic indices. From the method of derivation it is seen at once that this compound climatic index becomes larger (1) with increase in the values of the normal daily temperature efficiency indices for the average frostless season; (2) with increase in the length of the average frostless season; (3) with increase in the total precipitation for the average frostless season, and (4) with decrease in the total evaporation for that season. Conversely the value in question becomes smaller with lower daily efficiency indices, with a shorter average frostless season, with decreased rainfall, and with increased evaporation. According to this compound climatic index, northern humid and southern arid regions are represented as lying in the same climatic zone.

Root Growth of Opuntia versicolor at Constant Soil Temperatures,
by W. A. Cannon.

The temperature of the soil changes relatively slowly during the course of the day, and also the range is comparatively small, at the depths attained by the roots of most perennials of the Tucson region, including the cacti. Both of these conditions vary with the depth, among other features, and are accentuated in seasons of cloudiness and storm. In order to estimate the actual root growth of a plant, there-

fore, it is necessary to observe the rate of growth either at a constant temperature or with slight temperature range. Looking to this end, experiments were devised, of which the following is a summary of results now obtained, by which fairly constant soil temperatures were kept for periods of from 6 to 9 hours, during which time readings of root growth were made at intervals of from 30 minutes to periods of 3 hours each.

The series of experiments were conducted at the Coastal Laboratory, where in July the daily range of air temperatures is less than 10°C ., and the daily mean is about 20°C . The plants were grown in glass tubes sunk in thermostats of the desired temperature, while the shoots were exposed to air temperatures. In the first series a temperature varying not more than 1° from 32.5°C . was maintained. Typical results at this temperature, with readings made every 2 hours, were as follows: 1.2, 1.2, 1.6, and 1.3 mm. In another experiment the following root growths, also at 2-hour intervals, were noted: 1.1, 0.9, 1.7, and 1.0 mm. These results were substantiated in other experiments.

A second and a third series, differing from each other only in the temperatures employed, gave results of which the following are representative. In the second series a temperature of the soil was used which did not vary more than 1° from 25.5°C . The roots were exposed continuously to this temperature for 9 hours, and readings were made at intervals of 9 hours. The increase in length of the roots for each 3-hour period was as follows: 1.1, 1.1, and 1.5 mm.

In the third series of experiments the soil temperature varied less than 1.5° from 20°C . Observations were made every half hour. During the entire period, $7\frac{1}{2}$ hours, a total root growth of 1.8 mm. was made, which was slightly over 0.12 mm. for each half hour. An approximately constant growth-rate was maintained throughout the experiment.

From these experiments it appears that roots exposed from $7\frac{1}{2}$ to 9 hours to a fairly constant soil temperature do not exhibit measurable decrease in growth-rate; but although the total root-growth is at a rate somewhat different from that observed in other experiments, the results, on the whole, are confirmatory of those previously obtained. The probable rate of root-growth in the habitat of the species can now be calculated with some accuracy if the daily course of the temperature of the soil at the depth attained by the roots of opuntia is known. Other factors, such as aeration of the soil and behavior of the shoot, exert a minor influence.

Soil Aeration and Root Growth, by W. A. Cannon.

Observations on the root-systems of perennials growing in the vicinity of the Desert Laboratory show that they may occupy different positions in the soil. Some root-systems are deeply placed and others

lie close to the surface of the ground. Studies on the possible immediate causes of such characteristic differences in root habit indicate that the temperature and the aeration of the soil may both play important rôles. For example, the roots of *Prosopis velutina* and of *Opuntia versicolor* show unlike temperature relations. The roots of *Prosopis*, in short, react to lower temperatures than do those of *Opuntia*. Further, it appears from thermographic records that the temperature of the soil at a depth taken by the roots of the former species does not suit the more shallowly placed roots of *Opuntia*. It is concluded from these observations that the vertical distribution of the roots of these species is directly related to the vertical differentiation of the temperature of the soil. It appears possible, however, that the relation to soil aeration of shallowly placed roots may differ from that of roots that penetrate deeply. To test this possibility and to determine the immediate effect of a variable air-supply on the rate of root-growth, several experiments have from time to time been carried out. The results, which have not been entirely consistent, may be briefly given. Increased shoot and root growth followed artificial aeration of the soil in certain instances, while in others the aeration appeared to produce no effect. When, however, the roots of *Opuntia* were kept at a constant temperature, the results with this species were more consistent. For example, in one series of experiments, the roots of *Opuntia* were held at a temperature of 32° C. for 8 hours, during which time a slow current of air passed through the culture in 2-hour periods, with the alternating 2 hours in which the roots were not aerated. At the same time observation was made as to the rate of root-growth of a control of the same species which was not aerated. The leading results, in brief, were as follows: the average rate of root-growth for 2-hour periods while aerated, average of 13 observations, was 1.59 mm.; the average rate of root-growth of the same root not aerated was 1.25 mm.; the average rate of root-growth of the control was 1.3 mm. It would therefore appear that artificial aeration slightly increases the amount of root-growth of *Opuntia*. Further observations on the reaction of the roots of *Opuntia*, not here reported, indicate that an insufficient amount of air may inhibit root branching. It seems probable, consequently, that the superficial root habit assumed in *Opuntia* is due in part to the favorable soil temperature, and in part to the relatively favorable conditions of soil aeration.

Periodic Variations of Respiratory Activity, by H. A. Spoehr.

The investigations in this subject have been continued with special attention to controlling temperature. The plants used for study were kept in an electrically controlled water thermostat, so that the temperature of the air surrounding the plants did not range more than 0.02° C. in

a day, nor in the course of an experiment lasting 20 days. The optimum temperature for these experiments was found to be 27° C. The number of carbon-dioxide determinations made during a period of 24 hours was increased to 4 and in some cases to 6. An apparatus has been constructed which automatically inserts and withdraws the CO₂ absorption tubes from the air-stream at any desired time. Thus greater accuracy is obtained in the analysis of the air passing over the plants, and the amount of personal attention and labor involved in the course of an experiment is considerably reduced. A larger variety of material has also been employed, including a number of bulbous plants and the shoots from the potato, as well as several fungi cultures grown on gelatine, especially *Aspergillus niger*. All these plants show the same phenomenon: a higher rate of carbon-dioxide evolution during the day than at night; the difference between day and night is great on days of high solar radiation, while on overcast days this difference is but slight. The progress of the investigations has been somewhat interfered with by the unfavorable weather conditions of the winter and spring, and especially by not being able to procure from abroad some instruments necessary for the study of the electrical conditions of the atmosphere.

Studies in Photosynthesis, by H. A. Spoehr.

In the course of the last three years many experiments have been carried out with a view to reducing carbon dioxide by means of light and of experimentally testing the Baeyer formaldehyde hypothesis. By use of ultra-violet light from a quartz mercury-vapor lamp, solutions of carbon dioxide and of potassium bicarbonate were reduced to formic acid. The solutions of alkaline bicarbonates yielded the largest amount of formic acid, which seems to be due to the higher concentration of the HCO₃ ion in solutions of these salts. A direct reduction of carbon dioxide or carbonates to formaldehyde was never obtained, even in the presence of nascent hydrogen. A reduction of formic acid to formaldehyde by means of light also could never be accomplished. On the other hand, it has been possible to synthesize a sugar-like substance directly from formic acid by means of sunlight or ultra-violet light. This substance, which was obtained in the form of a sirup, has many of the properties of a sugar, such as the reduction of Fehling's solution and Tollin's solution. Algæ develop in solutions thereof in the dark, and can use the substance as an only source of carbon. This substance is undoubtedly a very complex mixture, analogous to formose. The chemical investigations are now in progress. It has been found that not only is this sugar-like mixture synthesized in the light, but light also easily decomposes it, so that the final yield is never large. In the decomposing action, besides formic acid, there is formed a volatile substance giving many of the tests for aldehydes.

In order to determine whether formaldehyde condenses to sugar under conditions such as possibly exist in the green leaf, an extensive series of experiments is in progress with solutions of formaldehyde and very weak alkalis in the sunlight and at ordinary temperatures. Thus far there is no evidence that formaldehyde could condense to sugar in the plant leaf in the sense of the Butlerow reaction.

Hydratation Capacity of Plant Colloids, by H. A. Spoehr and H. W. Estill.

Previous work on the diurnal variation of the acidity of succulents has shown the necessity of determining the effect of varying concentrations of acids and alkalis on the hydratation of plant colloids before any clear idea can be gained of the effect of light on the growth of these plants. An extensive study of the effect of acids and alkalis on the hydratation of the colloidal material of various plants is now in progress. It has become evident that the total swelling of plants like *Opuntia blakeana* and *O. discata* in dilute solutions of acids, alkalis, and salts represents the summation of independent reactions of various material to these reagents. Thus, solutions of acids, alkalis, and salts influence the swelling and growth of these plants by affecting: (1) the hydratation of the protoplasts; (2) the material that goes to make up the cell-wall and fibro-vascular system; (3) the permeability and osmotic properties of the plasma-membrane. It has been found that these three factors can act independently and even in opposite directions. Great differences were found in these respects in different portions of the same cactus joint and between young and mature ones; the colloidal material of the former showed much greater swelling than the latter in all solutions, and the excess of swelling in acid media above that in alkaline media or distilled water was much greater in the young joints. Of interest is the observation that the colloidal material from mature joints which have been freed as much as possible from the fibro-vascular strands showed a diminution in volume in weak alkaline solution.

The Behavior of Protoplasm as a Colloidal Complex, by Francis E. Lloyd.

The presence of large water vacuoles in the vast majority of plant cells converts them into osmotic systems in which the behavior of the emulsion colloids as such is masked to a greater or less extent. It is, for example, a difficult, if not impossible, task to evaluate the hydratation alterations caused by various reagents because of the total change in volume of the cell resulting from a gain or a loss of water by the vacuoles usually referred to osmotic interchange or to change in permeability. Among other purposes before the experimental cytologist, he has to account for such change in terms of structure of the colloidal complex called protoplasm. To eliminate errors of observation possible when water vacuoles, being a distinct system, chiefly composed of solid-disperse-phase and liquid-disperse-medium, are present, cells

have been chosen from which such vacuoles are absent. The protoplasts of many (though not all) pollen-grains appear to satisfy these conditions. These offer ready-to-hand material, with certain disadvantages indeed, but such as are not too serious. These are chiefly due to the presence of the more or less rigid envelopes (extine and intine). In the future it may be found quite possible to eliminate them by using younger material. For the present, the observations which follow have been derived from the study of mature pollen, for the most part of *Eschscholtzia californica*.

Many pollens burst on being placed in tap-water. When the protoplasm is thus set free, an internal secretion of water is begun, in consequence of which the whole mass becomes a froth, suggesting that the formation of water vacuoles in the growing cell is the result of growth and not a method of increasing pressure. Inasmuch as no vacuoles are present, the bursting depends entirely on the hydration capacity of emulsion colloids and not upon the presence of solutions of high concentrations, such as would be required to overcome the resistance of the envelopes. According to expectation, the hydrophilic colloids constituting the protoplasm behave in certain respects as, *e. g.*, do the hydrocellulose content of certain tannin cells and the analogous mucilage of the mucilage cells of mallows and cacti, which, when allowed to, may absorb water with sufficient avidity to burst the cell wall. Thus, the protoplasm of pollen will swell and may burst the envelopes even in solutions of high concentration, either after initial shrinkage or so quickly that an initial shrinkage may be assumed to occur, if indeed it does; *e. g.*, pollen of *Gossypium* bursts in 0.45/N KNO_3 in 50 per cent cane sugar and 25 per cent glycerol. Similar behavior is shown by other kinds. Even in concentrated salts (*e. g.*, KNO_3), glycerine, etc., the protoplasm swells sufficiently to distend the envelopes in the course of 15 to 30 minutes, though it is preceded by partial or complete shrinking. Weak acids and alkali cause swelling and (when the concentrations are proper) bursting and the formation of coagula characteristic of each reagent.

Pollen which will not burst at once in water may do so (*Lupinus*) after about 2 hours' germination, when the pressure becomes sufficient to overcome the resistance of the thin membrane just at the apex of the pollen-tube, and it is important to note that minute water vacuoles which are present in the tube protoplasm at the time have no measurable influence. The bursting of the envelope, therefore, serves as one index of the hydration capacity of the protoplasm, and, without disregarding others, serves to bring out many phases of behavior. The escaping protoplasm is variously distorted as it escapes, as a jelly would be under the same conditions, by the envelopes, and the observer is enabled to note the change or absence of change in the form of the suspensoids, and thereby to judge of their physical characters.

*Structure of the protoplast.*¹—The cytoplasm appears as a colorless, glistening mass. Only a very slight lack of homogeneity allows the inference of "granulation." No water vacuoles and no solids are visible. On applying a concentrated salt solution (3/N KNO_3) swelling slowly follows initial shrinkage, during which an emulsion-like structure is optically accentuated.

A lipid is present in amieronic dispersion and is apparently distributed throughout the whole of the cytoplasm. The alterations of surface tensions on swelling, on consequent pressure on the envelope (this being a possible factor), and on coagulation, causes changes in the degree of dispersion² and the lipid becomes segregated into visible droplets, which are usually smaller toward the periphery (in 0.7/N. NH_4OH) and frequently absent from a peripheral zone (in KNO_3 , 0.6/N). This behavior is strongly suggestive of that of the fluid disperse phase in relation to the fluid disperse medium of the protoplasmic emulsion colloid proper, and further that changes in permeability can be explained as changes in the size of the fluid suspensoids and in their spatial relations in the disperse medium.³ Such changes may be reversible, as when a previous volume, following shrinkage caused by a salt, is restored, or irreversible, as when coagulation has occurred. Alterations in permeability could thus be caused by mechanical pressure, or application of salts, or other dehydrating agent (such as glycerine), hydrating agents (acids, alkalis), heat, or any other conditions which would temporarily or permanently alter surface-tension conditions, or the amount of water held within the critical colloid complex. The "normal" condition of the protoplast is one adjusted to the substances present in itself and in the solutions within the vacuoles, if these are present, so that the application of (*e. g.*) distilled water or water of lower concentration must produce changes in hydration, and hence of permeability.

The mutual effects of two reagents, one a salt and the other acid or alkali, are of interest in this connection. A 10 per cent (or 1 per cent) solution of ammonia will cause the contents of a pollen-grain to escape in its entirety without visible damage (unless the swelling takes place too rapidly) in a few minutes. 3/N KNO_3 allows this swelling to take place only slowly, and just sufficiently in the stronger solution to cause rupture of the envelope. In the course of 40 minutes coagulation has set in. Similarly, 1/N HCl will first cause swelling (due to the initial diffusion of acid) and then coagulation, the intine being burst and the coagulum being more or less extruded in an irregular stream. In the presence of 3/N KNO_3 , the swelling is sufficient only to burst the extine,

¹These remarks apply to the cytoplasm of the vegetative cell, to which only attention has been paid till the present moment.

²Alkanet in alcohol-water, with minimum alcohol, was the reagent used.

³This view had occurred to Mr. E. E. Free at the time of a conversation with him during the progress of this work.

the intine remaining intact. The degree of dispersion must be different in the contrasted cases, and it is not impossible that such differences are analogous to those expressing changes of permeability.

The result of coagulation by one reagent is different from that caused by another. When the cytoplasm is irreversibly coagulated by formic acid, the gel, after drying, will swell less in ammonia than in formic acid. The coagulum formed in the presence of ammonia, which may be due to the pressure exerted by the envelopes on the swelling colloids, has a much softer consistency than that caused by acids. A coagulum is formed without more swelling than just sufficient to stretch the envelopes in very strong glycerine in the course of a few hours, and its consistency is again different from that caused by alkali. This coagulum will at once swell further and escape as a whole on the addition of ammonia, the volume of the coagulum being much greater than if caused by formic acid. Coagulation caused by acids takes place suddenly at certain concentrations of the reagent. It is always preceded by swelling, but this swelling is due probably to the lower initial concentrations which first reach the protoplasm.

The concentrations of acids and the consequent amount of swelling and the forms assumed by the coagula are so various as to prompt inquiry into the nature of their structure. One factor appears to be the resistance offered by the superficial layer of coagulum to further penetration of the reagent—this layer becoming a semi-permeable one. It would seem that the specific actions of acids on protoplasm may be due in part to coagulation effects imposed upon hydration, and this possibility is not confined to acids, since there is some evidence that alkalis may also have a coagulative effect at certain concentrations in addition to the power to cause swelling. Whether the ammonia is the immediate cause or not, it is certain that the protoplasm of pollen can be caused to coagulate in its presence, and similarly in the presence of potassium hydrate ($\frac{1}{1\frac{1}{2}}$ to $\frac{1}{2}/N$). Such behavior seems to be quite different from that of gelatine and similar colloids, so far as at present understood.

The evidence upon which the above is based supports the view that protoplasm is fundamentally a hydrophile emulsion colloid, of whose momentary interrelations of disperse-phase and disperse-medium its permeability is a function. The relation may be changed from moment to moment by hydrations and coagulations which, if irreversible, lead to death.

Chemical Changes accompanying Desiccation and Partial Starvation of Succulents, by E. R. Long.

The attempt to obtain individuals which would illustrate the metabolic changes taking place at intermediate stages of desiccation of succulents was begun in June 1914, when six healthy echinocacti were

taken up from the slopes west of the Desert Laboratory and placed on supports, three in the laboratory court exposed to full sunlight, and three within the laboratory in diffuse light in a room with a north exposure. The loss in weight was determined by weighing at intervals, and analyses were made after periods of approximately 5 and 8½ months of desiccation under the two sets of conditions.

The principal features of desiccation of the flattened joints of the opuntias native to this region being known to be something different from those presented by the globose echinocacti, it was deemed essential to follow a number of these plants through the earlier stages of depleted water-balance in order to compare the variations in weight and water-content with those observed in *Echinocactus*. The material consisted of 24 turgid joints of *Opuntia discata* taken from two plants growing near the chemical building of the Desert Laboratory on September 28, 1914. The separate joints were taken from terminal portions of the plant and were cut cleanly at the base in such manner as to be as nearly equivalent as possible in evaporative capacity. Six were arranged on a wooden support in an upright position in the open, exposed to the full illumination, the planes of the joints being north and south; six were placed near these, but in a horizontal position, being turned once every week, so that the two sides were alternately uppermost; six were similarly placed in an upright position in the diffuse light in the middle of the largest room in the main building of the Desert Laboratory, and six in a horizontal position.

The results of the analyses are as follows:

Prolonged confinement in diffuse light results in a decrease in density of sap in *Echinocactus*. Exposure in the open, with consequent rapid loss in weight, may be followed by an increase or by a decrease in the density of the sap.

Decrease in the density of sap is to be attributed to a disintegration of the carbohydrates, which, in *Echinocactus* No. 7, amounted to 13 per cent of the dry weight of the cortex. The destruction of material was extended to include the walls of whole masses of tissue in the cortex.

Increase in the density of the sap might result from rapid evaporation, which altered the proportions of water and dissolved substances, or by the addition of photosynthetic products.

The proportion of reducing sugars is greatest in the peripheral tissues of normal plants, in connection with the photosynthetic activity localized here, and decreases through the cortex to the central cylinder. The reduction which takes place in desiccation and starvation reverses the distribution of these substances, the greatest proportion after desiccation being found in the inner cortex and the total amount being reduced.

Non-reducing soluble sugars, which are present in only minute proportions, if at all, in normal echinocacti, are noticeable constituents of the sap of desiccated plants.

The acidity of the tissues is due to certain modifiable features of respiration. Acidity of plants which have undergone long-continued desiccation and starvation is low, since the amount of carbohydrate from which they are derived has been decreased.

Katabolism in extended desiccation and starvation eventually breaks down the plasmatic colloids and includes hydrolysis of the cell-walls of the cortex.

The loss in weight of *Opuntia* in full sunlight and in diffuse light is not very different during the first 35 days of exposure, and is practically the same after that length of time. The position of the flattened joints in the open may modify the rate of loss.

Opuntia desiccating in the open shows an increase in dry weight, but a decrease in hydrolyzable carbohydrate, while the acidity is not markedly different from the normal, though slightly less. Desiccation in diffuse light results in increase of acidity, increase of dry weight (not as pronounced as in the open), and decrease in hydrolyzable carbohydrate.

Reversible Changes of Form in Succulents, by D. T. MacDougal.

Gross measurements of joints of platyopuntias during their development and in succeeding seasons showed that these bodies were subject to reversible changes in length and width, as exemplified by the accompanying figures obtained from a joint of *Opuntia discata* (No. 3) at Tucson, in 1912, 1913, and 1914 (shortening indicated by bold-face figures):

Date.	Width.	Length.	Date.	Width.	Length.
1912			1913		
May 9	6.0 cm.	7.0 cm.	Mar. 9	15.3 cm.	17.2 cm.
May 18	9.8	11.0	May 9	15.2	17.0
May 29	11.2	13.2	June 18	15.3	17.0
June 9	11.8	13.2	1914		
Sept. 24	15.2	16.8	Apr. 3	16.2	17.2

A number of mature joints of this succulent were placed in bearing with precision auxographs of a type devised by the author in 1902, in which both expansions and contractions, magnified 20 to 50 times, are recorded. The changes of size of a mature joint, such as those indicated in March 1913, consist mainly of swelling by increased absorption of water made possible by disintegration of acids in the sap. This does not proceed at an even rate, but is most rapid in the first half of the day, being greatest from 11 a. m. until 2 p. m. During the remainder of the day this action would fall off and actual shortening might occur at night as a result of increased acidity and heightened transpiration. These reversible changes in form also take place in young joints,

and accompany growth, running parallel to its course and being determined in greater part by identical causes.

That the water balance is actually decreased at night and increased by day has been found by Mrs. E. B. Shreve, who says of a *cylindropuntia*:¹

"It was found, under conditions of average transpiration, such as occur in the greenhouse in summer, that the water intake at night is less than the outgo, while during the day the intake is greater than or at least equal to the outgo. . . . An examination of the water-content of stems from plants in the open and from the greenhouse showed that the highest water-content is at 5 p. m. after the close of a bright day, and the lowest just before daylight the next morning, with an intermediate amount at noon."

The Effect of Desiccation on the Structure of Echinocactus wislizeni,
by J. G. Brown.

The effect of desiccation on the structure of living tissues has been studied chiefly by zoologists who were interested in the ability of the rotifers and other invertebrates to survive extended periods of drought.

The capacity of plants, such as certain algæ, pteridophytes, and liverworts, to endure periodic drying, is even more remarkable than the ability of the rotifer to resist desiccation, but there is a paucity of literature on the changes of a cytological character in the cells of these plants resulting from conditions of drought.

The object of the investigation here reported was to determine changes in structure brought about by continued deprivation of water, and to discover any evidence of recovery on the part of the plant when, after a period of desiccation, it was again subjected to normal out-of-door conditions. Preliminary to the study of the desiccated material a careful examination of the structure of the normal plant was made. The principal conclusions warranted by the facts obtained are as follows:

Extended desiccation and starvation made no alteration in the integument of *Echinocactus*, but in a plant which had been thus treated for 73 months the cuticle was thicker than normal, while the outer walls of the epidermal cells were thinner. Cytoplasm and nuclei in the epidermal system were reduced, but new cork layers were being formed as in normal plants. Cell division was seen in the epidermal layer at the bottom of the grooves of the stem. The stomata remained permanently open and many were in a collapsed condition. Guard-cells of stomata differed from the normal in having the anterior walls thinner as compared with the posterior walls.

The palisade layer was thinner in desiccated than in normal plants of *Echinocactus*. The cytoplasm was reduced to small masses in the angles of the cells and the nuclei were variously deformed and reduced

¹Rept. Dept. Bot. Research, Carnegie Inst. Wash., Year Book for 1914, pp. 98, 99.

in size. Vacuoles had disappeared from the nucleoplasm and a thickened granular layer was present in the peripheral portion.

The most pronounced effects of desiccation and starvation were exhibited by the cortex of *Echinocactus*. The changes noted as having been seen in the palisade tissue were followed by the entire disappearance of the protoplasts and the hydrolysis of the cell-walls. The consequent disintegration of cell masses formed lacunæ as large as 8 c.c.

Some of the effects of desiccation and starvation were to be found in the medulla of *Echinocactus* plants under treatment, but to a lesser degree. Disintegration of cell-walls was observed in restricted areas. No change appeared to be produced in the vascular bundles by desiccation and starvation.

Early stages of the changes noted above, such as the reduction of cytoplasm and nuclei of cells, deformation and peripheral thickening of nuclei, and hydrolysis of cell-walls, were found in plants which had been desiccated in diffuse light for only 10 months.

An *Echinocactus* which had been desiccated for 42 months and then placed under normal conditions in the soil for 22 months did not entirely regain the normal condition. The epidermal system was fairly normal, excepting irregularity in proportional thickness of anterior and posterior walls of stomatal guard cells. Nuclei of the palisade cells were below normal in size, and only one was seen that had regained normal shape. The peripheral, thickened, granular layer was still present in many cases. The cortex also retained irregularities of cell-wall and nucleus, as effects of the starvation and desiccation. Recovery was most advanced in the outer part of the cortical region. Cell-walls in the outer cortex varied from 2 to 10 micra in thickness, while in the inner cortex the variation was from less than 1 micron to over 20 micra. The inner cortex of this recuperating plant was characterized by some nuclei which were larger than the normal.¹

The General Course of Depletion in Starving Succulents, by D. T. MacDougal.

A series of tests to determine the rate, course, and extent of the water-loss in massive succulents was begun in 1908. Selected individuals of *Echinocactus*, *Carnegiea*, and other plants with a relatively large water-balance, growing in the Tucson region, were taken from their habitats and placed upon stands which supported the plants at the height of a meter in such a manner that the light exposure was normal as to angle. Some were put in this position in the open, exposed to the full force of the sun, and were subject of course to the high midsummer temperatures of the region. Others were placed in laboratory rooms in which the illumination was from ordinary side-windows, and the temperature was rarely altered by artificial heat, being in general

¹See MacDougal, Long, and Brown. End results of desiccation and respiration in succulent plants. *Physiol. Researches*, vol. 1, No. 6, 1915.

under more equable conditions than that to which the plants in the open were subjected.

The course of desiccation under the conditions named has already been described in several papers. Certain features in the variations in weight of the plants under observation, however, remained without adequate explanation. Among these is to be included the fact that the rate of water-loss decreases more rapidly than the ratio of succulence, or proportion of water present to the area of the transpiring surfaces.

Among the survivors of the original lot of plants taken for the test was one large *Echinocactus* which had been taken from the soil in November 1908 and kept in a shaded room for more than 6 years.

The following conclusions as to the water relations of such large succulents are established by the examination of this material:

Echinocactus in diffuse light may lose as much as one two-thousandth part of its weight in one day, immediately following the excision of its root-system. The same plant 6 years later, under equivalent conditions, except that its weight had been reduced nearly a third, lost no more than 1 part in 17,000 of its weight in one day.

An *Echinocactus* weighing 38 kg., of which 90 to 95 per cent may be estimated as water, lost 3.5 kg., or one-tenth of its total water, in the first year of isolation in diffuse light. In the sixth year the loss was one-twentieth of the water-supply at the beginning of that year.

Echinocacti in the open lost 38 to 45 per cent of their original weight during the period from June to November inclusive. Individuals in the diffuse light of the experimental rooms lost 7 or 8 per cent in the same period.

Echinocactus is capable of growth in the apical region, in plants in which water-loss and disintegration of the carbohydrates (including hydrolysis of the cortical walls) has reached an advanced stage.

The rate of loss in weight of an *Echinocactus*, largely due to evaporation, is not correlated with the degree of succulence (proportion of amount of water present to superficial area of body) or with the density of the sap, but is to be attributed to morphological causes.

The difference in behavior of *Echinocactus* and *Opuntia* in desiccation and starvation is correlated with definite physical features. *Echinocactus* has a globoid stem consisting largely of thin-walled cells, in which the accumulated food-material is in the form of soluble carbohydrates. Solid material and accessory colloids are noticeably lacking. The flattened joint of *Opuntia* is composed of a network of fibro-vascular tissue. The fundamental tissue is rich in slime or mucilage, and somewhat higher in total hydrolyzable carbohydrates than is the fibro-vascular tissue. The loss of water from the large, globose stems of *Echinocactus* is much more affected by illumination than in the flattened stems of *Opuntia*. The course of respiration in the thin stems of *Opuntia* is such that acids formed during the process are present

in greater proportion and vary more widely through the day than in the large echinocacti. Some connection with the hydration of the slimes or mucilages is suggested.

Isolated individuals of succulent species survive varying periods when separated from a moist substratum. If the conditions for photosynthesis are inadequate, death may result from starvation. The disintegration of solid material in diffuse light may be such that the proportion of water in the tissues may be but little changed after several years of depletion.

SOME SPECIAL WATER RELATIONS OF PLANTS.

Plane Porous Clay Surfaces for Use in Atmometry, by B. E. Livingston.

The first porous-cup atmometer to be described was that of Bellani (1820), who employed what was essentially a porous cup with a plane circular upper surface and with the remainder of the wall impervious to water. The evaporating surface was that of a circular disk of porous clay closing the top of a metal cylinder, the latter filled with distilled water and connected to a reservoir below. This form of surface is exposed in practically the same manner as is a free water surface, yet the Bellani type of instrument encounters none of the difficulties met with in the operation of open pans of water. Nevertheless, this form of atmometer has failed to attract attention.

After some experimentation a satisfactory form of Bellani plate has been obtained, consisting of a circular disk of white, porous porcelain, 77 mm. in diameter, mounted across the large end of a glazed porcelain funnel. The apparatus is made as a single piece, the funnel and the disk being continuous and of the same material, but the lateral surface is heavily glazed externally. Wherever atmometric studies are to be related to water-loss from plane surfaces this modification of the porous cup may be employed.

Influence of Solar Radiation as a Drying Agent, by B. E. Livingston and E. S. Johnston.

Further progress toward the obtaining of satisfactory black porous spheres for the radio-atmometer has been made and a small number of usable pieces have been available for the summer of 1915. The black spheres heretofore obtained have generally proved unsatisfactory in various ways, and experimentation in the manufacture of these difficult pieces is being continued.

The records furnished by the radio-atmometer (a white and a black sphere operated side by side) in the open and in various intensities of shade have been critically studied for the summer climate of Baltimore and for that of Tucson. The instrument proves to be considerably more sensitive to the drying action of sunshine than is any plant so far tested, and it promises to be amply sensitive for ecological studies of solar radiation as a desiccating influence.

Auto-Irrigation of Pots of Soil for Experimental Cultures, by B. E. Livingston.

As has been reported, the porous-cup auto-irrigator furnishes a means for automatically maintaining the water-content of a given soil mass very nearly uniform for long periods of time, and it allows the ready measurement of the rate at which water is absorbed by the soil mass in question, as this rate fluctuates with the rate of water-loss by plant transpiration or by direct evaporation from the soil surface. With small amounts of soil and small plants one or more of the 12.5 cm. cylindrical cups used in the porous-cup atmometer have proved satisfactory, but the joining of a number of these small cups together, so as to avoid possibility of air-leakage, is somewhat uncertain, so that larger cylinders were desirable. These have now been obtained, the new size being about 5 cm. in diameter and 35 cm. long, thus allowing the use of a much deeper pot for the plant cultures than has heretofore been possible, without burying the stoppered opening in the soil. Placed horizontally, these larger porous cylinders furnish a satisfactory means for automatically maintaining the soil-moisture content in shallow culture-boxes.

The Progress of Wilting as Indicated by Foliar Transpiring Power, by A. L. Bakke and B. E. Livingston.

By means of the method of standardized cobalt chloride paper (a modification of the method of Stall) the march of foliar transpiring power was determined during progressive wilting of the plant. As the water-content of the plant decreases, foliar transpiring power decreases also, but as temporary wilting occurs and becomes more pronounced the rate of decrease in transpiring power becomes less rapid. At about the time when permanent wilting (in the sense of Briggs and Shantz) is attained, the value of the index of foliar transpiring power suddenly increases markedly, soon attaining a secondary maximum and then finally falling to zero, as the leaves die and desiccate. This secondary maximum in foliar transpiring power, as wilting progresses, has been pointed out by Leclerc du Sablon and others, though not in exactly this connection. Its detection by means of hygrometric paper may be of value in determining when permanent wilting actually occurs, or the occurrence of this secondary maximum may be taken as a criterion for detecting the physiologically critical point for which permanent wilting has been an approximate criterion.

Foliar Transpiring Power and the Darwin and Pertz Porometer, by S. F. Trelease and B. E. Livingston.

The direct method of measuring the transpiring power of leaves by means of standardized cobalt-chloride paper was employed in a study of the diurnal march of this physiological condition in leaves of wandering Jew (*Zebrina*) grown in the greenhouses of the Laboratory of

Plant Physiology of the Johns Hopkins University. Simultaneously, and with similar plants, the diurnal march of the permeability of the leaves to air-flow under pressure was also studied, by means of the F. Darwin and Pertz porometer. This instrument is calculated to measure the degree of stomatal opening from time to time, and if this feature is indeed the controlling condition in its operation, then the results obtained should be capable of interpretation to show the diurnal march of stomatal diffusive capacity in the sense of Brown and Escombe.

The results obtained from these parallel series of observations are similar in that both methods agree in showing the same kind of daily march, the values of both indices rising to a maximum in the day and falling to a minimum in the night. The range of variation, however, between the minimum and maximum is generally somewhat greater for the indices of stomatal diffusive capacity (derived from porometer readings) than for those of transpiring power (derived from the hygrometric paper tests). It appears that the porometer readings do furnish data for deriving the stomatal diffusive capacity, at least in these *Zebrina* leaves, but that this diffusive capacity can not be considered as quite proportional to transpiring power, as has been pointed out from earlier studies carried out in cooperation with the Desert Laboratory and as has been emphasized by Renner, conditions other than that of stomatal diffusive capacity are surely influential in determining foliar transpiring power. It is clear, however, that stomatal capacity is the main condition influencing transpiring power in such leaves as were here used.

It should be emphasized in this connection that transpiring power and the actual rate of transpiration are not at all the same thing; the former represents simply the group of *internal* conditions influencing the latter rate, which is of course greatly influenced also by a group of external conditions, such as the evaporating power of the air, etc.

The Autonomic Movements and Water-Relations of Cacti, by Edith B. Shreve.

The results obtained in previous years on movements of stems of *Opuntia versicolor* have been further tested and extended to other species of cacti. The data have been divided into two main parts, the first of which traces the causes of the movements as far as changes in turgidity, which are in turn due to periodic differences between water-intake at the roots and water-loss by transpiration; the second includes extended measurements of transpiration and of water-intake, which were undertaken with the aim of finding the causes of the variations in these phenomena. The first part has been made ready for publication and contains the following summary:

(1) Ten species of *Opuntia* and also *Carnegiea gigantea* have been found to show seasonal movements of the branches, which consist of a drop during desiccation and a rise during subsequent recovery, and these movements have been correlated with turgidity changes.

(2) The form of the adult cactus plant and the position of its branches are determined by the water-relations existing during the period of growth and secondary thickening of its various parts and not by any peculiarities residing in its growing-point or its mode of initiating lateral branches.

(3) *Opuntia fuscicaulis*, *O. leptocaulis*, and *O. versicolor* were measured for a short-period movement, which consists of an upward movement during the daytime and a downward movement at night, under normal conditions of temperature, light, soil, water-content, and evaporative power of the air.

(4) A detailed study of *O. versicolor* showed that this short-period movement is influenced by temperature, light, evaporative power of the air, and the water-content of both soil and tissues, separately as well as in various combinations. But the influence of these factors is an indirect one, acting through other intermediate processes.

(5) The day-to-night movements have been shown to be caused directly by turgidity changes in the stems.

(6) *O. versicolor* is less turgid at night than in the daytime, as is shown by the fact that the plant absorbs more water through its roots in the day than it loses in the same time by transpiration, and at night it loses more than it absorbs. This is the opposite of the behavior shown by non-succulents which have been studied.

In this paper no mention is made of a possible correlation between acidity and the movements, because further experimentation has thrown doubt upon the existence of such a correlation, and surely shows that if a relation exists it is by no means a simple one. In the Year Book for 1914 (page 98) it was said:

"Plants were placed under controlled conditions where an increase or decrease of acidity could be predicted and their movements measured . . . a downward movement was always accompanied by an increase in acidity and an upward movement by a decrease in acidity."

The predictions referred to were made on the basis of the results of other workers; but later, when tests were made on the material used for the experiments, it was found that the acidity changes under conditions of high temperature and darkness did not agree with the predictions. Consequently the statement quoted above from last year's report does not hold for all conditions of temperature and light.

The acidity results which were obtained from this work show that, at least for the time of year when the tests were made (April to June), *O. versicolor* shows a marked increase in acidity when kept at 90° F. in darkness for 8 to 16 hours. Plants were placed under the controlled conditions at the close of hot, clear days. Many determinations were made, so that there is no doubt in the mind of the experimenter about the correctness of the results for the conditions and material

used. The non-conformity of the results with those obtained by Dr. H. M. Richards on the same material (see Year Book 1911, p. 66, and 1912, p. 66) is probably due to a difference in the stage of metabolism which existed at the time the plants were placed under controlled conditions. Until this matter is given further investigation it is obviously impossible to draw conclusions regarding the relations existing between acidity changes and movements, or acidity changes and transpiration.

Data from the transpiration studies, the second main division referred to above, are now being assembled and include the results of many new experiments as well as those reported upon last year. The following is a provisional summary of the results as far as they have been elaborated:

(1) Progressive desiccation of soil and tissues in *Opuntia versicolor* is accompanied by a change in the relative transpiration (transpiring power). This change is of such a nature that, while relative transpiration is greater by night than by day when the plants are turgid and supplied with plenty of water, by the time extreme desiccation is reached the relative transpiration for the day is greater than for the night. The change in relative transpiration is brought about largely by a decrease in the absolute night transpiration.

(2) Experiments with severed joints show that it is the water-content of the tissues which determines the transpiring power and that the water-content of the soil is responsible only as it influences the condition of the tissues. The characteristic day-to-night changes in transpiring power take place for several days after the joints have been cut from the roots; consequently, it can not be changes in the amount of water absorbed which cause changes in the transpiring power.

(3) Simultaneous measurements of water-intake at the roots and of transpiration show that, under normal turgid conditions, transpiration-rate is not the major factor governing the amount of intake.

(4) Thus, from the results given under 2 and 3 above, it appears that there exists some internal factor, or factors, controlling both transpiration and absorption.

(5) The absorption capacity suggests itself as a possible internal factor causing changes in water-intake and transpiration. Measurements of the amount of distilled water absorbed by cylinders of tissue cut from the stem show that water-absorbing capacity of the tissues is correlated positively with the water-intake by the roots, and negatively with transpiring power. So far these measurements have been made for plants under normal conditions only.

(6) Further experiments confirm the statement that, under normal conditions of light and temperature which exist during the 24 hours, cylinders of tissue cut from joints show the greatest swelling capacity when their acidity is lowest, and vice versa.

(7) The acidity changes in these plants at high temperatures make necessary an investigation of the absorbing capacity of tissues which have been kept under certain controlled conditions, before any conclusions can be drawn concerning the connection between acidity and the transpiration or root-absorption behavior.

The Relation of Altitude and Habitat to the Transpiring Power of Plants,
by Forrest Shreve.

During the month of June 1915 work was begun upon the relative transpiring power of some 30 species of perennial plants of the encinal region of the Santa Catalina Mountains. The method of standardized hygrometric paper, recently elaborated by Livingston, was employed, making it possible to secure readings in the field from plants growing in their normal environment. The species used in this work were selected with a view to representing all of the physiological types in this richly diversified vegetation, and also with a view to being able to compare the transpiring power of the same plant at different elevations. In order to make adequate comparisons between different plants it was found necessary to take an hourly series of readings throughout the day on each of the individuals investigated. The hygrometric-paper method was found inadequate for the measurement of the low transpiration-rates of *Agave*, *Yucca*, and *Opuntia*, although a very thin grade of paper was used. It was also impossible by this method to measure the water-loss from the upper sides of the leaves of several sclerophyllous trees. In these cases comparisons were secured for the lower surfaces alone, while in the majority of cases the behavior of upper and lower surfaces was averaged.

Differently situated individuals of the same species, growing at the same altitude, were found to exhibit differences of transpiring power—the plant in situations of highest soil-moisture content having the highest coefficients. Species characteristic of the streamways, and confined to them, were found to have much higher coefficients than the species characteristic of the adjacent upland and slopes. Among the different types of plants investigated at 5,000 feet, marked differences were found in the coefficients of transpiring power and slight differences in the daily march of the coefficients. When plants of the same species were compared at different elevations, but in similar topographic sites, there were found to be differences in the coefficients and also in the daily march. In a comparison of the behavior of the mesquite (*Prosopis velutina*) the maximum is found to occur earliest at 2,400 feet (8 a. m.), later at 4,400 feet (10 a. m.), and still later at 5,000 feet (11 a. m.). The behavior of *Calliandra eriophylla* is similar in having an early maximum at 2,400 feet, but some individuals at 5,000 feet exhibit a late maximum coincident with that of evaporation. A comparison of the bellota (*Quercus emoryi*) at 5,000 and at 6,000 feet showed the highest

coefficient of transpiring power to precede the highest evaporation at the former elevation and showed the two to coincide at 6,000 feet.

These data confirm our knowledge of a check to the rate of transpiration which is applied before the daily maximum of the evaporative power of the air. This check appears to be applied later and later in the day with increasing altitude, and to be eliminated at 5,000 feet for some species and at 6,000 for others. The actual rates of water-loss, and sometimes even the coefficients of transpiring power, are higher at the lower altitudes. The "reduction of transpiration," of which so much has been said regarding desert plants, is not to be discovered in the maximum absolute water-losses, which are greatest in the desert plants, but is to be detected in the time of the daily check in rate.

ENVIRONIC RELATIONS: PHYTOGEOGRAPHY.

The Osmotic Pressure of Vegetable Saps in relation to Local Environmental Conditions in the Arizona Deserts, by J. A. Harris.

An extensive series of cryoscopic determinations of the osmotic pressure of saps of four principal growth-forms, trees and shrubs, dwarf shrubs and woody twiners, perennial herbs, and winter annuals, characteristic of the foot-hills, cañons, cliffs or rocky slopes, bajadas, arroyos, and saline areas, was made for the purpose of ascertaining whether or not any definite relation between sap-density and environment prevails. The data secured indicate that the lowest osmotic pressure is to be found in the sap of plants from the arroyos. As might be expected, the highest concentrations were found in the plants of the salt spots. Eight determinations of plants from this habitat gave an average of 37.1 atmospheres, but a very wide range of variation is exhibited among the species as well as within any single species.

The species of the bajadas without exception stand next to those of the saline areas in concentration of sap, and the lowest concentrations are to be found in the plants taken from the beds of the arroyos or washes. The principal results are summarized in the following table:

Osmotic pressure in atmospheres of growth forms in five habitats of the Tucson region.

Growth forms.	Arroyos.	Cañons.	Rocky slopes.	Bajadas.	Salt spots.
Trees and shrubs.	17.7	22.4	22.0	34.7	47.9
Dwarf shrubs and twiners.	16.6	21	21.1	23.9	34.2
Perennial herbs.	13	14.4	16.8	19.7
Winter annuals.	12.9	13	15.3	21.1	23.6

Climatic Cycles and Succession, by F. E. Clements.

The further analysis of the fundamental processes and principles of succession has led to a clear recognition of the distinction between the ontogeny and phylogeny of plant formations. The ontogenetic process is represented by the unit succession or *sere*, in which develop-

ment begins with a bare area—rock, water, or soil—and progresses slowly but inevitably to a climax. The latter is regarded as the organic unit of vegetation and hence is designated by the term “formation.” The climax or formation is a mature or adult form, the development of which is seen in the successional sequence. The nature and permanence of the climax are determined by climatic control. As a consequence, each formation persists until an effective change of climate causes its disappearance in the old region with its concomitant invasion into a new one, or until it gives rise to a new flora through evolution. Such changes are phylogenetic in nature, and are of the first importance in unraveling the successions of the geological past. Thus, as in the case of the individual plant, ontogeny in vegetation comprises the periodic reproductive process of the formation as an organism under the same climate, while phylogeny deals with the change of one climax into another, or its differentiation into two or more under the stress of the changing climate.

The phylogenetic study of plant formations, *i. e.*, the course of succession in the geologic past, has been made possible only by the recent great advances in climatology. The existence and recurrence of climatic cycles has been established beyond question, and it has proved possible to recognize a complete series of such cycles from the familiar annual one through sun-spot and deformation cycles of varying duration and intensity to the grand deformation cycles extending over millions of years. Each of these has an appreciable effect upon vegetation, but the major cycles alone are able to produce phylogenetic changes. The phylogenetic events of the first importance in the history of vegetation are those recorded in the evolution of new floras and hence of climax units, characteristic of the four great vegetation eras, viz, Eophytic, Paleophytic, Mesophytic, and Cenophytic. Hence, it is possible to recognize four primary periods in the terrestrial history of vegetation and to divide the geosere, which comprises the whole course of succession on the globe, into corresponding eoseres, namely, Paleosere, Meseosere, and Ceneosere. The flora of the first was pteroid, and it seems probable that several climax formations were already differentiated, corresponding to the respective dominance of Cordaites, Lepidodendreae, and Calamites. The dominants of the Meseosere were gymnospermous, and the number of climaxes seems to have increased with climatic differentiation. The Ceneosere was initiated by the change from gymnosperms to angiosperms, and the course of the succession began to approximate that which is seen to-day. The eosere of the Eophytic period is wholly hypothetical, but the conclusion is unavoidable that it was marked by climaxes of a bryophytic or pteridophytic nature.

Next in importance to the phylogenetic changes which characterized each era, were those produced by the glacial-interglacial cycles of

great periods of glaciation, such as the Permian and the Pleistocene. Instead of the evolution of a new flora and new climaxes, each advance and retreat of the ice produced a corresponding shifting of the climax zones in front of it. This shifting of the zones by which each was first replaced by successively earlier or lower preclimaxes, and these in turn by successively later or higher postclimaxes, constitutes a clisere, *i. e.*, a successional development from one climax to another. The clisere differs from the eosere in that no new flora is evolved, but existing climaxes merely shifted, and differs from the sere in being a succession of climaxes instead of developmental stages which terminate in a relatively permanent climax. The consistent application of developmental principles has confirmed the original assumption that all features of vegetation are the structural results of developmental processes, and hence furnish direct evidence of the operation of the latter. This has long been known to be the case in hydroseres, where the successional movement from open water to the climax is relatively rapid and symmetrical. However, these have been thought to constitute exceptions and not to furnish the rule. The careful scrutiny of climax formations throughout western North America during the last three summers has shown the principle to be of universal application, in time as well as in space. Even in the most static community, not only have the relations of the various dominants and subdominants been found to record the past development and to suggest that of the future, but it has also proved possible to recognize developmental areas throughout, minute and fragmentary as they often are. This is especially true in the climax zones of mountains, where surface and soil are extremely diverse and where great differences occur in the smallest contiguous areas. This successional analysis of dominance has made it clear that no two dominant species are exactly alike in their demands, while it has justified their grouping into communities on the basis of the similarity of their responses. From this has come the far-reaching conclusion that the dominant furnishes the key to the developmental study of vegetation, as well as the chief objective of the experimental attack which must accompany the latter. This has been definitized in the concepts of the consocieties and the consociation, which are respectively developmental and climax communities controlled by a single dominant. Consocieties fall naturally into developmental units, or associates, and consociations into climax units or associations, both of which are due to similarity of physiological response. Thus, the recognition of the dominant as the basis of investigation has made it possible to utilize both autecologic and synecologic evidences in the study of vegetation, and to harmonize them both in terms of development.

A Successional Study of the Transitions between Climaxes, by F. E. Clements.

The use of developmental methods in the analysis of the climax formations of western North America has been continued during the summer of 1915. For a number of reasons, especial attention has been given to the transition zones between climaxes, particularly grassland and scrub, which cover the largest areas and show the greatest complexity. It has been found possible to standardize the results of such study for purposes of comparison by dealing directly and chiefly with the dominants and subdominants, *i. e.*, consociations and societies, of the contiguous climaxes. The first transition studied was that from the subclimax and climax prairies of eastern Nebraska and South Dakota to the short-grass plains of western Nebraska and eastern Wyoming. The alternation of dominants was first traced through northern Nebraska and parts of South Dakota to the plains, and then eastward through the sandhills of eastern Nebraska to the prairies again. The second region traversed was from northeastern Kansas to western Oklahoma, southward through the Panhandle of Texas to the Pecos River, and northward through eastern New Mexico to the Great Plains. The change from the *Bouteloua-Bulbilis* grassland to the *Prosopis-Aristida* savannah was first traced southward through Texas, and then checked in the reverse direction through New Mexico. A similar study was made of the transition between the desert scrub of the Southwest and the sagebrush formation of the Great Basin. This was first traversed from south to north from southeastern California to Nevada and Utah, then southward through eastern Utah and northward through western Colorado. Consequently, the successional relations of the climax dominants were noted scores of times, within as well as between successive climaxes. This not only afforded a constantly recurring check on the developmental history and the regional limits of the different climaxes, but also furnished decisive evidence of their climatic relations, especially with reference to the effect of future cycles. In this connection, much attention was paid to the competition responses in the ecotone between two or more dominants, and suggestive results were obtained in the attempt to use these responses as an index of present as well as of future climatic tendencies. Finally, an endeavor was made to test more rigorously the assumption that the habitat, like the formation, has a developmental history which ends in a permanent or mature condition determined by the climate.

The Vegetation of a Desert Mountain Range as Conditioned by Climatic Factors, by Forrest Shreve.

The work on the vegetation and physical factors of the Santa Catalina Mountains, which has been in progress for five years (see previous annual reports), has been elaborated up to the close of 1914 and published. The principal aim of this work has been to correlate the cli-

matic gradients of the mountain with the vertical differences of the vegetation. The mountain is characterized by desert on its lower slopes, by open evergreen-oak forest or encinal at its middle elevations, by pine forest above 7,000 feet, and by fir forest on the highest summits. Nearly all the species of plants are distributed so definitely with relation to altitude and habitat as to indicate that they are controlled in their movements and establishment by the operation of physical factors. The major differentiation of vegetation on the mountain is controlled by the factors which are in turn due to differences of altitude. The minor influences of slope-exposure and other topographic features cause local departures from the normal altitudinal gradient of vegetation, but these departures are merely such as to bring a given type of vegetation to an altitude higher or lower than that in which it is commonly found. Rainfall, soil-moisture, evaporation, and temperature have been studied at a series of stations reaching from 3,000 to 9,000 feet, at 1,000-foot intervals. The influence of slope-exposure on the conditions of soil-moisture and evaporation and the influence of topography in modifying the theoretical conditions of temperature have been particularly emphasized. The rainfall at the forested elevations is about $2\frac{1}{2}$ times as great as it is on the desert, and the soil-moisture in the driest portion of the year is from 5 to 15 times as great, according to the slope-exposure. The evaporation is 3 to 4 times as great on the desert as it is on the summit of the mountain. The daily and seasonal temperatures are approximately 30° F. lower on the summit of the mountain than on the desert, while the frostless season is about half as long in the former as in the latter locality.

The ratio of evaporation to soil-moisture in the Santa Catalinas has already been commented upon (see Annual Report, 1912), and it appears to be the climatic feature which limits the distribution of the mountain plants at the edge of the desert. The upward limitation of desert plants appears, on the other hand, to be due to the operation of winter temperature conditions. It has been necessary to study the vertical gradient of temperature with special reference to the operation of cold-air drainage, which is very pronounced throughout the lightly forested or unforested portions of the mountain. For instance, the difference between the minimum temperature in the floor of a cañon at 6,000 feet and on the summit of a ridge at the same elevation has been as great as the normal difference between two stations of the same topographic site located nearly 3,500 vertical feet apart. Comparisons have been made between the climatic gradients of the Santa Catalinas and gradients derived from the Weather Bureau stations of southern Arizona, situated at different elevations in the valleys of the adjacent region. These comparisons are particularly significant with respect to the rainfall conditions, showing that the isolated mountains have a greater rainfall at 4,000 and 5,000 feet than localities in

the valleys at the same elevations. The coldest temperatures of winter at 8,000 and 9,000 feet are much milder on an isolated mountain, surrounded by desert, than they are at the same elevation on extensive plateaus. These and other features of the work on the Santa Catalinas have emphasized the difference between the altitudinal gradient of physical conditions on a small mountain and on a larger gently tilted plain which lies through the same elevations. The relation of environmental conditions to the vegetation is likewise different in the two. Both of these cases form an important part of the general problem of the relation of vegetation to climate.

The Vegetistic and Floristic Features of the Pinaleno Mountains of Southern Arizona, by Forrest Shreve.

During September 1914 an expedition was made from Tucson to the Pinaleno Mountains (Mount Graham), in Graham County, Arizona. These mountains are 60 miles distant from the Santa Catalinas, reach an elevation of 10,500 feet, and are built chiefly of gneiss. The object of the visit was to compare the general vegetistic features of these two desert mountains, which are of approximately the same age, in nearly the same state of dissection, and constructed of the same mineralogical material. The gently rolling summits of the Pinaleno range lie chiefly above 9,500 feet and are clothed with a fir and spruce forest much greater in extent than the analogous portion of the Santa Catalinas. The numerous cañons which have eaten the edges of the summits are very precipitous. This circumstance has limited the extent of the pine forests and has presented conditions favorable for the high occurrence of the trees and shrubs which are characteristic of the encinal, or evergreen-oak, region. The existence of well-watered cañons and steep slopes has caused a pronounced interdigitation of the highland and lowland vegetations, so that the plants of streamways are carried nearly 1,000 feet lower than they are in the Santa Catalina Mountains, while the encinal is carried about 1,200 feet higher than it extends in the Santa Catalinas.

The existence of lofty and sharply dissected alluvial aprons on the northeast side of the mountains, falling to an elevation of 2,800 feet at the Gila River, and the existence of a sub-level plain on the southwest side, lying at 5,500 feet, causes marked dissimilarities in the vegetation of the lowest slopes on the two sides and also influences the vertical limits of the vegetations on the two faces of the mountain.

Inasmuch as the Pinaleno Mountains had not been visited by botanists for 40 years (since the Whipple Expedition), a full collection of all plants in suitable condition was made, with the cooperation of Professor J. J. Thornber. Many plants of the Sonoran-Sinaloan region, characteristic of the lower elevations of the Santa Catalinas, were not found in the Pinaleno Mountains, while in the higher elevations of the

Pinalenos were found many plants common to the Rocky Mountains of northern New Mexico, but not in the Santa Catalinas. Some of the latter species are found in the Pinaleno range only at elevations greater than any in the Santa Catalinas, but the great majority are found at elevations which do exist in the latter range. Owing to the similarity of climatic and other environmental conditions in the two mountains, the absence of these species from the Santa Catalinas would appear to be due to causes other than those of the physical environment. It will at least be possible to test the ability of these species to survive when an extension of their ranges is attempted.

Distribution of the Cacti with reference to the Rôle Played by the Relation of Root Response to Temperature, by W. A. Cannon.

Studies on the reaction of the roots of the cacti to certain environmental features, particularly the temperature of the soil, indicate that the root-temperature relation may be of special importance among the complex factors which determine the geographical distribution of the family.

Numerous garden cultures and experiments, carried on at the Desert Laboratory and the Coastal Laboratory, show that the species of cactus from the Tucson region require a relatively high temperature for an effective growth-rate of the roots. For example, the average hourly increase in length of the roots of *Opuntia versicolor* has been found to be about 0.3 mm. at 20° C., 0.6 mm. at 30° C., and 1.0 mm. at 34° C. At a temperature of 16° C., however, a growth-rate of only 0.07 mm. was observed.

The period in which the soil-moisture and temperature is suitable for the active growth of the roots of *Opuntia versicolor* and other cacti, in the vicinity of the Desert Laboratory, is restricted to about six weeks of each year. This is limited both by soil-moisture and soil-temperature. At a depth of 15 cm. the mean maximum temperatures for midwinter and midsummer of a typical year were 8.1° and 34° C., respectively. The mean maxima at a depth of 30 cm. were 12.2° and 33° C. for January and July. The course of soil-moisture, as shown by numerous studies, is such that there are two moist and two dry periods each year. The moist periods are in winter and in summer. In the intervening seasons, particularly in the fore-summer, the soil at a depth of 15 to 30 cm., or that occupied by the roots of the cacti, carries an insufficient amount of moisture for root absorption. From these environmental conditions it happens, therefore, that in winter low soil-temperatures prevent root-growth, and in the earlier part of summer the soil is not sufficiently moist for the growth of roots. In short, it is not until the coming of the rains of midsummer that in the Tucson region the roots of the cacti experience conditions favorable for their growth. Root-growth of the cacti ceases with the coming of autumn

either because of excessive dryness of the soil or because of its low temperature.

From the observations on root-growth and root-relations of the cacti as summarized in the foregoing paragraphs it appears that the presence of the cacti in the Tucson region is in large part to be attributed to the occurrence of rains at a season when the soil is also warm. These observations, also, make it possible to suggest that a similar root-soil relation may obtain among the cacti of other regions, explaining on the one hand their presence in such regions, and suggesting on the other the causes for their sparseness, or absence, in yet other regions where they might be expected to occur.

The cacti occur mainly in the southwestern United States, in the uplands of Mexico, and in Central and South America. A feature of the climate of the regions inhabited by the cacti is the relatively scant rainfall, which also is periodic. Whatever may be the character of the winter climate, that of the summer season is marked by more or less precipitation. Thus, at Tucson, for example, about 54 per cent of the annual rainfall is in summer. At Tehuacán, on the Mexican plateau, which has been characterized as the richest region known in cacti, 72 per cent of the precipitation is in summer. In portions of Central and South America where the cacti occur, rains constitute a feature of the climate of the warm season. We may therefore make the generalization that in regions inhabited by the cacti their presence is in large part to be related to the coincidence of precipitation and high temperature, by which favorable growth conditions, particularly of the roots, are insured.

In regions where the rainfall either is relatively light or wanting in summer, and cacti occur to a limited extent, it is not impossible that the summer rainfall is not the minimum for the species, or that the species are adjusted to a lower temperature relation than that found in the cacti in southern Arizona. The latter alternative prevails with *Opuntia ramosissima* of the Mohave Desert, as indicated in another section, as well as that of certain extra-regional cacti, not here reported.

Rate of Root-Growth of Opuntia ramosissima and its Possible Ecological Significance, by W. A. Cannon.

Opuntia ramosissima is native in the Mohave Desert. An important characteristic of the climate of this desert is its low annual rainfall, only 14 per cent of the total occurring in summer; and it has been shown in another section that a relatively low summer rainfall does not favor active root-growth. The fact that cacti occur in the Mohave Desert, therefore, suggests special conditions. Among the possible factors which might operate to bring about the survival of cacti in the Mohave, one only need receive attention here, namely, the possibility that the root-soil temperature response is such as permits this species

to develop in the winter rains. In this case it would point either to a relatively warm winter soil or to a somewhat different temperature response than that already found in the cacti of southern Arizona. To test the validity of the latter possibility, a series of experiments was planned in which the root-growth of *Opuntia ramosissima* was to be compared with that of *O. versicolor*, from the vicinity of the Desert Laboratory, as a control.

In the experiments each series was continued about 8 hours at soil-temperatures varying between 19° and 31° C. as extremes. The range of temperatures employed and the variation were probably about what the species experience in their proper habitats. The following summary of the experiments can be given:

Experiments with *Opuntia versicolor*: (1) With soil-temperatures ranging between 21° and 27° C., the root-growth, in 8 hours, was 2.1 mm. (2) With temperatures from 19° to 27.5° C., the root-growth was 2.3 mm. (3) The root-growth at temperatures between 23° and 30° C. was 2.7 mm.

Experiments with *O. ramosissima*: (1) The root-growth, in 8 hours, at soil-temperatures between 19° and 27° C. was 3.3 mm. (2) At soil-temperatures between 19° and 27° C. the root-growth was 3.2 mm. (3) At temperatures ranging between 19° and 25° C. the root-growth was 1.8 mm. (4) The root-growth at temperatures between 23° and 31° C. was 3.4 mm. (5) At temperatures between 20° and 25.5° C. the growth was 4.2 mm.

These experiments, and others, indicate that the roots of *Opuntia ramosissima* at soil-temperatures below "optimum" and above 19° C. increase at a somewhat faster rate than do those of *O. versicolor* at the same temperatures and under the same conditions. The difference in rate between the two species is approximately 33 per cent.

Further studies on the reaction of the roots of *O. ramosissima* to soil-temperatures under 20° C. indicate that the minimum temperature for efficient growth-rate is probably lower than in *O. versicolor*. For example, in 2-hour periods, and at soil-temperatures ranging from 12° to 17° C., the roots of *O. ramosissima* increased 0.2 and 0.5 mm. in length, while those of *O. versicolor* grew, in one case, 0.1 mm., and in another not at all.

It would appear, therefore, from these observations, that the roots of *Opuntia ramosissima* from the Mohave Desert grow somewhat more rapidly at parallel temperatures than do the roots of *O. versicolor*; and, especially, the roots of the Mohave species appear to have a fairly active growth-rate at relatively low temperatures. It would not seem impossible, therefore, that the roots of the species in the Mohave Desert (1) grow during seasons of relatively low temperatures, and (2) that the roots may penetrate the ground relatively deeply.

EREMOGRAPHY: THE SALTON AND MOHAVE DESERT REGIONS.

The Recession of the Salton Sea, by D. T. MacDougal.

A series of gage-readings of the level of the water is taken weekly by officials of the Southern Pacific Railway, and the data have been sent to this Department. It appears from these records that the recession was but 2 inches in July 1914, 19 inches in August and September 1914, 5 inches in October 1914, 6.5 inches in all during the following November, December, January, and February, 7.5 inches in March and April 1915, 4 inches in May 1915, and about the same in June 1915.

The total for the year ending July 1, 1915, was about 50 inches, which is about the average annual recession for several years previous, but is more than in the previous year. The erratic rate of recession is to be attributed to local rains and to the overflow from irrigation systems. The irregularities noted above make it difficult to follow the occupations and successions of the beaches now being exposed.

It is to be noted that the calcium deposition indicated by the chemical analysis no longer takes the form of deposits on stems and other emersed objects.

Composition of the Salton Sea Water, June 8, 1915, by A. E. Vinson.

The annual analysis of the water of Salton Sea has not been completed at this time, but several determinations of considerable interest are available. The total solids have increased 16.8 per cent and now amount to 1,377.4 parts per 100,000. This is somewhat less concentration than has occurred in former years, but a considerable volume of fresh water flowed into the Sea from the Colorado River last winter. The constituents that have been determined are given in the following table:

Composition of Salton Sea Water, June 8, 1915 (in parts per 100,000).

Total solids	1377.4
Sodium	441.60
Potassium	5.12
Sulphuric (SO ₄)	174.47
Bicarbonic (volumetrically) ¹	16.62
Carbonic total (gravimetrically) ¹ (11.98 CO ₂)	11.92
Oxygen consumed ¹	0.208

¹Determined by Dr. H. A. Spoehr.

The elements show a fairly uniform concentration from year to year, with the exception of calcium and potassium. Calcium has been deposited in the form of tufas, but the history of potassium is less evident. In 1912 there was no concentration of this element and the following year there was a loss, although sodium had concentrated 18.8 and 19.3 per cent, respectively, for the years under consideration. In 1914 the disappearance of potassium, which had been so evident for several years, ceased, and this element showed almost the normal

concentration. During the past year potassium has been coming back and shows a rate of concentration far in excess of that of the other constituents. The fresh water received from the Colorado probably accounts for this in part, but more likely potassium has been returned to the water by the decay and disintegration of organic forms and of tufas that had been deposited by them. The behavior of potassium is shown very strikingly by the potassium-sodium and the potassium-total solids ratios in the last two lines of the table given below:

Annual composition and rate of concentration of certain constituents of Salton Sea water.

Year.	Solids.		Sodium.		Potassium.		Calcium.		Magnesium.		Sulphuric SO ₄ .		Ratio K:Na 1:48.3.	Ratio K:sol- ids 1:158.
	Amt.	Inc.	Amt.	Inc.	Amt.	Inc.	Amt.	Inc.	Amt.	Inc.	Amt.	Inc.		
		<i>p. ct.</i>		<i>p. ct.</i>		<i>p. ct.</i>		<i>p. ct.</i>		<i>p. ct.</i>		<i>p. ct.</i>		
1907	364.8	111.05	2.30	9.95	6.43	47.60		
1908	437.2	17	134.26	20.9	2.78	20.8	11.87	19.2	7.63	18.7	56.74	19.2	1:48.3	1:157
1909	519.4	16	160.33	19.4	3.24	16.5	12.70	6.9	8.96	17.4	65.87	16.0	1:49.5	1:160
1910	603.8	21	189.28	18.0	3.53	8.9	13.67	7.6	9.84	9.8	76.36	15.9	1:53.6	1:171
1911	718.0	19.0	227.81	20.3	3.81	7.9	15.62	14.2	11.68	18.7	91.67	20.0	1:59.8	1:188
1912	846.5	17.5	270.71	18.8	3.81	0.0	17.28	10.6	13.62	16.7	106.83	16.5	1:71.1	1:222
1913	1,002.6	17.7	323.08	19.3	3.45	-9.4	19.75	14.2	16.22	19.1	124.65	16.6	1:94.0	1:288
1914	1,179.6	17.5	381.47	18.8	4.01	16.2	22.22	12.5	19.03	17.3	148.10	18.0	1:95.1	1:294
1915	1,377.4	16.8	441.60	15.7	5.12	27.6	174.47	17.8	1:86.0	1:269

Interpretation of Travertine Record of Blake Sea, by D. T. MacDougal and Godfrey Sykes.

An outlying mass of fragmental granite projects from a spur of the Santa Rosa Mountains into the Cahuilla Basin in southeastern California, the crest of the rocks rising above the ancient shore-line of Blake Sea, which filled the basin to a level something above that of present high tide in the Gulf of California.¹ This cape is designated as "Travertine Point" in our publications, as the surface of the granite boulders is covered to a varying depth with dendritic and lithoid tufa. Some marks and figures, presumably carved by Indians in the travertine, have long been known and were seen by us on our first visit to the place in 1906. In the continuation of our work on the Salton Sea it was realized that these figures might possibly yield some evidence as to the duration and variations of the ancient Blake Sea and of the smaller modern Salton Lake.

A visit to the formation was accordingly made in March 1915, and a careful inspection showed that the number of carvings on the rock was very large, and that some, made in the earlier layers of travertine, have been coated over to such depth that they may be made out only in the most favorable illumination or shading. Others show as deep furrows with weathered surfaces, visible at a hundred yards or more, while none of recent origin have yet been found.

¹See plate 1, The Salton Sea. MacDougal *et al.*, Carnegie Inst. Wash. Pub. No. 193. 1914.

A slice of the travertine extending across four lines of a complex pictograph and down to the granite base was cut out and the surfaces of the sample are now being polished and prepared for critical examination by skilled lapidaries in London under the personal supervision of Mr. Sykes. It is now clear that the carvings were not made in the granite, but in the travertine, and extended study may be necessary to determine the depth at which the figures were made and what deposition and weathering has since taken place. This fact favors the presumption that Blake Sea was a fluctuating body of water and not a continuously receding one. The final proof of the matter will rest chiefly upon biological evidence concerning the activities of organisms in connection with the deposition of tufas to which the botanist may be expected to contribute. The whole body of evidence to be obtained by the study of this material promises to be of prime importance in determining the climatic cycles and geological successions of plants in the Mohave Desert region.

General Features of Vegetation in the Mohave Desert, by Forrest Shreve.

In the autumn of 1914 and the spring of 1915 a general reconnaissance was made of the vegetistic features of the Mohave Desert and of the region which lies between it and southern Arizona. The Mohave Desert is dominated by an open stand of microphyllous shrubs, and the principal differentiating feature of its climate is the occurrence of rain only in the late winter and early spring. The area is sharply contrasted with the Tucson region, where the succulents form such a large element in the vegetation and the chief climatic feature is the bi-seasonal rainfall. The more elevated portions of the Mohave Desert adjacent to the fringing mountains of its southern and western boundaries are characterized by a richly diversified assemblage of shrubs, by the arborescent *Yucca*, and by a small number of cacti. Throughout the remaining portion of the area, below an elevation of 4,000 feet, the dominant plants are *Covillea tridentata* and *Franseria dumosa*, and over extended areas these are often the only perennials to be found. *Covillea* occurs in all topographic situations and in a wide range of soils, in marked contrast to its more restricted occurrence in the vicinity of Tucson. *Franseria* is not wholly coextensive with *Covillea*, being very uncommon on slopes which have rock *in situ*.

It is true of the Mohave Desert in general that the minor topographic features are without a marked influence on the character of the vegetation. For example, the open stand of *Covillea* on a bajada is usually found to extend without any modification onto the adjacent slopes of the mother mountain; the shrubbery found along small streamways is no more dense than it is elsewhere and contains no distinctive species; the edges of dry lakes can be approached without change in composition or density of vegetation up to the lake bed itself; the north and

south slopes of hills and low mountains are also without differences of vegetation. These statements are not true of the more elevated parts of the Mohave, but each of them holds true below about 4,000 feet, and in all of the features mentioned the Mohave area differs greatly from southern Arizona, where all slight topographic differences are accompanied by dissimilarities in the vegetation. It is only in the largest mountains that the vegetation exhibits a differentiation due to altitudinal climatic changes. Many mountains which rise 2,000 to 3,000 feet above the desert floor are strikingly similar to the desert itself in their vegetation. The bajadal slopes are also identical through a vertical range of 3,000 feet. The principal vegetistic differences from an elevation of 4,000 feet down to the level of the Colorado River lie in (1) the dissimilarity of the texture and perhaps of the soluble mineral content of the soils which lie nearest the dry lake-basins and those which lie nearer the surrounding hills or mountains, and in (2) the special features of the sandy areas. The fine alkaline soils which lie nearest the dry lakes are covered by *Atriplex*, while the coarser and presumably less alkaline soils of the bajadas are dominated by *Covillea* and *Franseria*. Areas with sandy soil always exhibit differences from adjacent non-sandy areas, even when the two are topographically equivalent. The most striking features of the sand are the low and open stands of *Covillea* and *Franseria*, the presence of perennial and annual grasses, and the great abundance of ephemeral herbaceous plants.

The most striking feature of the vegetation of the Mohave Desert, so far as investigated, is the slight amount of habital differentiation which it exhibits. This condition is closely related to the severity of the physical environment and to the highly specialized behavior of the few species of dominant plants involved in the vegetation, each of which is capable of enduring a wide range of conditions.

Climatic Changes, by Ellsworth Huntington.

A preliminary reconnaissance of the principal basins in the Mohave Desert region and to the northward was made during the earlier part of the year. The purpose of this work was to determine whether more detailed study another year will furnish an adequate basis for a climatic scale extending from the Tertiary to the present time, and sufficiently accurate to serve as a standard of reference for other parts of the world. Such a scale has been prepared by Penck, for example, on the basis of glaciation in the Alps and elsewhere. Glaciation, however, tends to destroy the records of past events more than to preserve them. Hence the attempt to use it as the basis for determining the number, nature, and probable duration of periods having one kind of climate or another is fraught with great difficulty. In a desert region such as that which drains to Death Valley, on the contrary, the records of past events

are subject to a minimum degree of destruction. The general tendency is to preserve the evidence of one period by covering it with the deposits of another. Thus long series of deposits are formed which contain a full climatic record, if only it could be read. In most desert regions such records are accessible only in small fragments where their borders have been eroded, or by means of deep borings which of necessity disclose the nature of only a minute portion of a given deposit. In the Death Valley drainage area the deposits are fortunately eroded to an unusual depth in many places, or else have been upturned by recent faulting, and can be studied with great ease and thoroughness. There is, perhaps, no other part of the world where the prospects are so bright for obtaining a complete record of all the climatic changes, both large and small, from the later part of the Tertiary era through the entire glacial period to historic times.

In addition to the main purpose of framing a climatic scale, the present work in the Death Valley drainage area serves two other purposes. One is to test the old criteria for the determination of past climatic conditions and to devise new criteria. The other is to determine the relation of each new fact to the various hypotheses advanced in explanation of climatic changes. Only a preliminary reconnaissance has in most cases been possible during the present year. One of the most important lines of study, namely, a correlation of the glacial phenomena of the Sierras with the various types of evidence in the desert at their base, has not yet been begun.

The Effect of Climate versus Earth Movements, by Ellsworth Huntington.

Terraces and other alluvial deposits are of special importance as possible evidences of climatic changes, because no other type of evidence seems to be so widely spread. The great difficulty in interpreting them lies in the fact that similar features have repeatedly been supposed to be the result of movements of the earth's crust. The Mohave Desert is a particularly good region in which to study the matter. On the south the desert is bordered by the great San Andreas fault, along which the San Francisco earthquake took place, and on the west by the still greater fault at the eastern base of the Sierra Nevadas. Along both lines extensive movement has taken place in recent times. Hence here, if anywhere, terraces due to earth-movements ought to be well developed. Yet such is not the case. Although most interesting and peculiar features have arisen along the fault zones, terraces are not important except where the climatic conditions are appropriate according to the hypothesis set forth in "Explorations in Turkestan" and "The Climatic Factor." A phase of this problem has been investigated by Mr. Free, as described below.

An Ancient Bajada of the Great Basin Region, by E. E. Free.

Brief announcement of certain generalizations concerning the bajadas or débris-aprons of mountain ranges in the Great Basin and in the arid regions generally was made in the report of this Department for 1914. The essential conclusion was that these bajadas appear to be composed of distinct superposed elements and to indicate a record of alternating erosion and deposition around the mountain base. Further work has been confirmatory of this generalization and has brought out, in a striking way, the great development, wide distribution, and uniform character of the third, or sub-Recent, of these superposed bajadas. This surface has now been identified in all parts of the Great Basin and has been traced in nearly all of the major river valleys and over many of the mountain passes. It constitutes one of the most important physiographic elements of the Great Basin region, and its remarkable smoothness and regularity of grade suggest its completion during a long period of substantially uniform conditions.

Stream-cuttings into this ancient surface are everywhere of the flat-floored, steep-sided type previously described. The base to which these newer cuttings is graded seems to differ little, if at all, from that of the ancient surface, the difference being rather one of the curvature of the gradient. This fact and the uniformity of the physiographic elements over an area so wide and so varied make it impossible to consider the physiographic changes as the result of structural movement, changes in lake-levels, or other local causes. It is very probable that the cause lies in climatic changes and that significant evidence regarding the course of these changes can be obtained by closer study of the physiographic elements described.

The ancient bajada is well developed on the northern slope of the San Bernardino Mountains at the southern border of the Mohave Desert, southeastern California. Here the Mohave River has cut a typical steep-sided channel through the beds of the ancient bajada and these beds are exposed for a horizontal distance of over 100 miles. An intensive study of this area is in progress, and especial effort is being made to discover paleontological evidence which will enable the determination of the age of the ancient bajada.

The Stages of Development of Playas, by Ellsworth Huntington.

The temporary lakes known as playas are peculiarly well developed in the area draining to Death Valley. Some are completely flooded to a depth of a foot or more every year. Others contain large areas which have not been flooded for centuries, and which are being eroded by the wind. Some are floored with clay, and others with deposits of every degree of salinity up to almost pure crystals. Two important problems present themselves for solution. The first is the determination of the physical character of playas in various stages. In the

area under discussion it will probably be possible to find almost every stage of development, and thus to form a typical series to which playas in other parts of the world may be referred. The second, and more important, problem relates to the chemical composition of the deposits. The various chemical precipitates, such as soda, potash, lime, gypsum, borax, and others, which are laid down when salt lakes evaporate, are most puzzling because they do not follow the laws which seem to be deduced from laboratory experiments. The presence of minute organisms is doubtless in large part responsible for this, but the reduction to the playa stage with its alternate drying and flooding may be an important factor. The marked climatic fluctuations indicated by other lines of evidence suggest that the playa stage has been much more common than is generally supposed.

The Curtailment of Rivers by Desiccation, by Ellsworth Huntington.

Three main rivers, the Mohave, Owens, and Amargosa, drained to Death Valley at the height of the glacial period. Practically no surface water now reaches it. The process by which each of the three rivers has been cut off is typical of what has happened in almost every arid region, and therefore needs no elucidation. Owens River reached Death Valley through a chain of from three to five lakes, which were greatly expanded at the time when the river was largest. The Mohave and probably the Amargosa appear to have had few or no lakes along their courses at the time of their maximum development. Now, however, they are again and again interrupted by lakes or playas which owe their origin to the deposition, by tributaries, of detrital material in the form of fans.

The Agreement of Botanical, Chemical, and Physiographic Evidences of Climatic Pulsations, by Ellsworth Huntington.

Perhaps the most important single feature of the year's climatic work has been the correlation of diverse types of evidence in respect to the climatic changes of the past 2,000 years. A study of the chemical composition of the salt water of Owens and Pyramid lakes, by H. S. Gale and J. C. Jones, shows that the lakes must have overflowed and been fresh not much more than 2,000 years ago. Old strands indicate that the fall from the outlet level has been pulsatory, that is, the lake level has fallen, then risen toward, but not generally to, the old level, and then fallen again. This has been repeated several times. A comparison of the strands with the curve of growth of the sequoia tree which grows only 50 miles from Owens Lake, shows that the periods of high water in the lakes correspond closely with those of rapid growth in the trees. The correlation is so close that it is possible to date a given strand within a century or less. Moreover, the same series of strands can be detected not only at Owens and Pyramid, but at Mono Lake,

which had no outlet. This suggests that in time we may be able to assign approximately correct dates to all the score or more of strands around the various lakes. This will go far toward giving a correct time-scale for the climatic variations of post-glacial time.

In addition to this, the character of the various strands gives a clue to the kind of climate prevalent at any particular period. For example, the strand of 1350 A. D. indicates particularly stormy conditions with phenomenally high winds, a conclusion which agrees with historic accounts of western Europe.

The Death Valley Series, by Ellsworth Huntington.

As a basis for work in the immediate future, Death Valley furnishes a peculiarly inviting field. The bottom of that deep depression has alternately contained a lake or playa, or has been dry for protracted periods. The evidence of this is found in a series of thousands of feet of clays alternating with gravels. Toward the end of the glacial period, at a time not yet determined, these deposits were uplifted and tilted in such a way that they are exposed for many miles and can easily be studied. A preliminary examination suggests that they present a record of several glacial *epochs* preceding the four which are usually recognized as constituting the last glacial *period*. There has not yet been time to work out the full series, nor to ascertain whether any beds are repeated by faulting. It is certain, however, that the deposits point to even greater climatic complexity than is indicated by the phenomena of glaciation. The only known series at all comparable is the uplifted lake beds of Seistan in eastern Persia, which are described in "Explorations in Turkestan." The Death Valley beds are better than those at Seistan, for they are thicker and pass into solid rock at their base. The change from soft clays to solid rock, together with other changes which take place at that point, suggest not only that the end of the Tertiary era was marked by a great transition, as is generally recognized, but that the transition was extremely rapid and that the biological effect must have been correspondingly intense. Further study of these beds from the physical, chemical, and biological considerations is of the greatest importance.

GENETICS AND VARIOUS SPECIAL INVESTIGATIONS.

Transmission or Recurrence of Environic Effects in Phytolacca,
by Francis E. Lloyd.

Certain effects, such as distortion and discoloration of foliage (obtained at Carmel) and morphological alterations of inflorescences and contained structures (obtained at Tucson), allowed the test of their inheritability. (See report for 1914.) The first generation from plants with abnormal foliage has shown no indication that the condition is inherited. On the other hand, one individual of the parent

generation, grown under glass, produced normal foliage early in the season, while later leaves show the abnormal characters. Examination of the affected areas of the leaf shows that within them the secondary physiological responses of the palisade and sub-palisade tissues have been suppressed and the structure remains therefore in an embryonic condition. This would seem to indicate that we are dealing with a "physiological" disease.

Negative results have also followed from the study of the second (F_1) generation from seeds produced by abnormal green fruits of the Tucson plant No. 1. All the progeny appear normal at present.

This year a departure from the normal, consisting in the production of very narrow lanceolate leaves, was synchronously entered upon by a small number of plants (in lot No. 131) at Tucson and Carmel. While this may be an expression of the general leaf-distortion above and previously noted, the only feature noticeable is the change in shape due to the reduction of the transverse measurements.

The Genetic Analysis of Guayule (Parthenium argentatum) under Cultivation,
by W. B. MacCallum.

When a wild plant is domesticated and transferred from a natural state to the condition of intensive cultivation, new forms make their appearance sooner or later. The cause of this occurrence of new varieties is not altogether clear. They may be forms already existing unobserved in nature, or they may be variations that would have occurred any way, and not necessarily caused by the environment of cultivation. To what extent the direct influence of the conditions of domestication may induce permanent variations is not apparent; indeed, many exclude this altogether as a factor in the origin of new varieties. The absence of accurate record, however, and the obscurity of time have left a very inadequate knowledge of the behavior of plants in this respect when first brought into cultivation. In *Parthenium argentatum* we have the unique case of a plant, not only brought suddenly into domestication from a wild state, but from extremely arid and desert conditions to an environment of intensive cultivation in a region of exceptionally favorable climatic conditions, grown in very large numbers, and every step a matter of most accurate record.

In the dry and rather stunted condition in which the desert plants usually exist it was difficult to determine with certainty more than two or three unquestioned varietal forms, although many differences, especially in regard to size and habit, were discernible that did not seem to be altogether environmental. Grown under culture, however, with uniformity of soil and other conditions, the differences of environment are largely eliminated and the recognition of strictly varietal differences becomes easier. Over 100 different forms, quite distinct from one another, have been isolated. Between some the differences are slight,

though distinct and clear-cut, but in most cases the differences are so pronounced and conspicuous as to be recognizable at considerable distances in the field. The differences exist in practically every character of the plant, such as size, color, arrangement of the flowers, time of flowering; shape, size, color, arrangement of leaves, general habit of the plant, as erect, diffuse, open, compact; ranging from tree-like erectness to procumbent. In size the differences are very remarkable, the extremes being as 25 to 1. In such characteristics as the secretion of oils, tannin, resin, etc., there are also striking differences—in some varieties one or more of these being present in a pronounced degree and in others almost entirely absent. Such a character as the winter condition of the leaves affords opportunity for conspicuous variations. The leaves ordinarily are quite persistent through the winter, giving the plant every appearance of an evergreen, but some forms tend to drop many of their leaves in the winter and become partially deciduous, and the extreme is reached in at least one case, which is absolutely deciduous.

As the plants are pollinated by minute insects crawling about in the flowers, it was naturally expected that cross-pollination would be of frequent occurrence and that many of the different forms would prove to be of hybrid origin and would follow the usual custom of hybrids in the segregation of characters. This complete permanency, however, of all the varieties argues against the idea of their hybrid origin. Assuming them to be mutants, we would expect them to breed true, as they do. Pure cultures of practically all the varieties are being maintained and any mutations that may occur will be observed. So far none have been recorded. It is quite improbable that the plant has reached the end of its capacity to originate permanent variations, and although all of the hundred or more varieties now existing originated previous to their being brought under cultivation, we can look with some confidence to at least some continuation of this process under observation.

All attempts at cross-pollination between different varieties have thus far given no results. That they are, at least in a large measure, sterile to one another is evident. To what extent hybrids are possible, and between what varieties, and their behavior, are questions yet to be determined.

The Rôle of the Factors in a Desert Complex in Evolution Processes in Leptinotarsa, by W. L. Tower.

During the present year, substantial structures (of reinforced concrete and cypress) have replaced the temporary ones hitherto used. In addition to the new arrangements for the actual experiments, a complete system of water-pipes supplies each cage, saving much time and wastage of water and in other respects contributing to the efficiency

and economy in the operations. In addition, a small but commodious record building has been erected and equipped, and also concrete cellars with heavy double covers, provided for the installation of the recording instruments, protecting them from the weather and reducing the instrumental error as well as the dangers of damage to the instruments. In all respects the plant, as now constructed, gives greater security and is far more efficient than the previous arrangements.

The winter of 1914-15 showed another possible mode of action of the desert complex upon its inhabitants, for the cold, wet conditions inflicted (in all of the cultures) a heavy loss, roughly estimated at the present time at about 90 per cent. This loss was uniformly of the extremes in all the hibernating populations, so that the different extreme types isolated (for tests of this year) in the last generation of 1914 were eliminated. This is in accord with many other experiences at the Desert Laboratory during the course of these investigations, and I have had the same results in nature in experiments in the tropics in Mexico and at Chicago. It thus seems that the eliminating action in a population, together with its relation to the mean or modal group, is rather constant, regardless of the nature of the factors of elimination. In this process there is an element of conservation rather than one of diversification. In all of these experiences in elimination I find that a freshly isolated divergent group is, rather uniformly, entirely eliminated, while one that has been isolated for two or more generations is not eliminated, as it has apparently undergone some population adjustment and established a mean that is able to meet the diverse eliminating factors to which it is subjected. Interesting data have been collected, in the course of the experiences at the Desert Laboratory, upon which it will be possible to base an experimental analysis of this problem. There can be no reasonable doubt that these relations are of the highest importance in the establishment of species and groups in nature and in their distribution and ecological relations. In spite of the heavy eliminations, no losses of any moment were sustained in the cultures.

In 1912, 1913, and 1914 report was made upon the alteration of the water relations in *L. decemlineata*. The tests which were made in the winter of 1914-15 show almost the same results as hitherto; the stock was returned to Chicago for hibernation. Tests to determine whether this alteration is reversible have shown, as the result of breeding the Tucson lines at Chicago for two generations before hibernation, that a small percentage may be able to pass the northern winter (0.1 to 0.5 per cent), but in subsequent seasons these have not been able to develop a race that has the cold-resisting capacity of the original stock. Apparently, the alteration is slightly reversible, but more slowly, and possibly not to the original condition. Tests of the inheritance of this alteration in 1914-15 gave the same results found in previous years.

These cultures of *L. decemlineata*, reared continuously through many generations under desert conditions, are beginning to show other changes in color, in pattern, in sculpture, and possibly in reactions or behavior. Many show slight alterations; some tested in the laboratory at Chicago are permanent, others are not so permanent, and the entire series gives one the idea of being subjected to some disturbing processes that have not yet gone far enough to manifest themselves in pronounced changes or to indicate just what is to be the outcome. Present indications are that in these series of cultures we are observing the effects of the continuous pressure of the medium upon the race. I hope that these lines can be continued long enough to give some experimental basis for opinion upon this problem, and unless some accident happens the present equipment renders the prospects for this much greater than in previous years.

The mutating stem stocks noted in previous reports, although largely reduced by the winter's elimination, so that the surviving populations were all close to the mode of the group, have continued to show the production of mutants in each generation, one that appeared being a further alteration of one that had previously been obtained. This series of cultures and its mutant products have now been sufficiently tested with regard to their production in nature at Tucson and in the laboratory at Chicago to determine the type of behavior and its method of production. Six more of the mutants have been subjected to genetic testing and analysis during the past year at Chicago, so that the constitution of several of them is now partly known. None of these have so far shown any new gametic agents, the mutants in every instance being due to combinations of agents that entered into the original stem stock from the parental species. Although no new gametic agents have been discovered, and may not be produced by this process, it is obviously one that, operating in nature, would produce no end of heterogeneity and give an opportunity for the establishment of independent new specific groups.

Within the last three years a new inheritable type of modification has appeared, which concerns fundamental alterations in the stripes upon the elytra, of a kind and extent not known in any of the original species. This series of changes, which now are found in nearly all of the mutating stem stocks, arises slowly by small variations and in many respects seems to be due more to environment than to the mutating process which the stocks show, although it is not possible in this series to distinguish clearly the causes.

Cultures of these elytral modifications tested in the laboratory at Chicago show complete genetic stability, a high degree of dominance over the normal, and (what is more interesting) a sort of orthogenetic progression, simpler conditions being followed even in pure lines by more and more complicated conditions of pattern arrangement.

Some rather complex pattern types have been extracted, and these are in some cultures already giving more complex conditions, so that there is no means of knowing how far the process will go. The tests being made of these alterations at Chicago are under standard and uniform conditions, in which at the least the usual environmental action is eliminated, but in spite of this the apparent orthogenetic progression continues by what appear to be some series of internal operations that are gradually working themselves out, giving stable pure lines during the process. Collectively the series shows a wide array of new conditions due, as far as present evidence goes, to the introduction of some new gametic factors and the gradual production of the possible combinations between these and the existing factors.

No new cultures have been introduced at Tucson during the year, owing to the derangement of the investigation by the building operations and the poor transportation to and from the tropical areas whence many of the desired introductions come. The political conditions in Mexico also seriously hinder the investigations, it being quite impossible to obtain from the southern part of Mexico materials much needed.

The general oversight and care of the experiments has been continued through the year by Mr. J. G. Sinclair.

Relationships and Distribution of the Cactaceæ, by N. L. Britton and J. N. Rose.

At the time the report on the progress of this investigation was written last summer, Dr. Rose was engaged in exploring the cactus deserts of western South America, one-half of the expense of this expedition being borne by the New York Botanical Garden. He returned in November 1914, having secured notes, photographs, specimens, and living plants of most of the cacti which inhabit Peru, Bolivia, and Chile; his field studies and subsequent museum work have demonstrated the existence in these regions of several hitherto unrecognized genera of Cactaceæ and a number of undescribed species. The collections made by Dr. Rose were extensive, and their study and description occupied much of the time of both research associates during the winter and early spring, but substantial progress was also made in writing descriptions of other cacti, preparatory to the publication of the monograph of the family. Many additional drawings and paintings have also been secured.

Dr. Britton gave part of the month of March 1915 to further studies of the cactus region of Porto Rico, visiting most of the area inhabited by these plants along the southern coast of that island and obtaining additional information on geographic distribution.

In last year's report reference was made to the desirability of exploring also the cactus regions of eastern South America, and through a continuation of cooperation with the New York Botanical Garden Dr. Rose proceeded in May to eastern Brazil, making Bahia his first base of

operations; he next carried the work into Argentina, and returned in October, having made an immense collection of living plants and prepared specimens, together with much systematized information.

Dr. Rose was much impressed with the similarity of the cactus flora of the vicinity of Bahia to that of the West Indies. He remarks in a letter to Dr. Britton:

"I have been greatly surprised at the close relationship between the flora of Bahia and that of the West Indies, for there has been a general understanding that the two were quite distinct. This is strikingly true in the cacti and there is good reason to believe that it is equally true in other families. This relationship is much closer to the West Indies than to the west coast of South America. The species of the two regions are quite distinct, but many of the genera are the same."

We had already known that the cacti of the Venezuelan coast and of the Dutch Islands near that coast had some affinity with West Indian types, as is also indicated by the present incomplete knowledge of other groups of plants, and this knowledge, taken together with the observations of Dr. Rose about Bahia, lead us to believe that an exhaustive study of the flora of the whole northern coast of South America with relation to West Indian affinities would be a very valuable contribution to geographic botany.

As regards further field work, before closing the present cactus investigation, it is desirable that Ecuador and Venezuela be visited, that some further studies be made in Arizona and New Mexico, and that another expedition be made to Southern Brazil and Argentina. Cordially proffered cooperation by Professor J. J. Thornber, of the University of Arizona, is gratefully acknowledged, as also the contribution of valuable specimens by Mr. W. H. Long.

The Immediate Effects of the Injection of Reagents into the Ovary in Toreniaournieri, by Francis E. Lloyd.

Torenia possesses an embryo-sac, one end of which, containing the egg-apparatus, protrudes much beyond the mouth of the ovule. On general grounds this genus therefore appeared to afford material peculiarly suitable for ovarial treatments. It has eventuated, however, that so far as methylene blue is concerned, the progress of events is as in *Scrophularia* (see previous report). The study has thrown some additional light on the mechanism of the embryo-sac, especially of the egg-apparatus. The structure of the ovule is essentially that of *Scrophularia*. It has, however, a longer funicle, and the exostome is directed toward the placenta. The protuberant end of the embryo-sac lies roughly parallel to the funicle and its conical free end lies normally against a placental pollen-tube "conductive tissue" of papillate cells with strongly mucilaginous free walls. The embryo-sac is therefore free only in a morphological sense and in practice it is difficult to reach

the egg-apparatus directly by means of watery solutions lying within the locule. Furthermore, the embryo-sac is invested by a cuticle which is discontinuous only for a small area at the apex, at which point the gelatinous ends of the synergidæ protrude. Only at this point might watery solutions find ready entrance but for the above-mentioned conditions. When the ovules are dissected out and bathed with tap-water, the synergidæ absorb enough water frequently to burst inwardly with respect to the embryo-sac, the vacuole disappearing. It may also happen that the bursting results in extrusion of the synergidæ from the apex of the embryo-sac. The delicacy of adjustment of the sexual mechanism thus indicated is further demonstrated by the fact that the cells of the egg-apparatus and endosperm are plasmolyzed by a solution of potassium nitrate slightly more concentrated than 0.1/N. In plasmolysis, the protoplasmic membrane, proper to the endosperm, lying against the egg-apparatus is withdrawn therefrom, while the vacuoles disappear by contraction from the egg and synergidæ. It is this behavior which shows that the entrance of the water into the embryo-sac is through the uncuticularized apex. The difficulty of applying a watery solution to the unprotected embryo-sac is apparent.

It is, however, possible to reach the egg, as in *Scrophularia*, by injecting the ovary. The course of movement of methylene blue lies through the funicle and chalaza, and accumulation occurs in the tapetum, a layer of cells investing the antipodal moiety of the embryo-sac. From this region the reagent passes along the embryo-sac to the egg-apparatus. That this behavior is perfectly definite is shown by the fact that it is identical with that in orthotropous ovules, of which a few are usually found in each ovary.

The course of the pollen-tube is as follows: Passing along the mucilage cells of the placenta, it attacks the embryo-sac at the uncuticularized apex, passing down between the tips of the synergidæ to reach to the egg-cell. The egg meanwhile loses its vacuolated structure, its whole volume being occupied, the protoplasm having the appearance of that of the pollen-grain. It is doubtful if fertilization involves the destruction of one or both synergidæ by the pollen-tube.

Development and Persistence of the Fruit in the Cactaceæ,
by Duncan S. Johnson.

Work on this problem has been pursued during the current year at Johns Hopkins University, and from April to September at Tucson and Carmel. As in the past, chief attention has been devoted to the origin, the anatomy, and the fate of the persistent fruits of *Opuntia fulgida*. Studies have also been made of the persistence and proliferation of the fruits of other species of *Opuntia* and to the development and distribution of the flowers of the giant cactus.

Seeds of *Opuntia fulgida* were germinated at Baltimore to seedlings a centimeter long. The germination of these seeds has not hitherto been reported, so far as is known. It evidently occurs but rarely in the field and was accomplished in the laboratory only after part of the seed coat had been cut or filed away. Careful search among the fruiting plants of *O. fulgida* at Tucson in April failed to reveal any plantlets that could be shown to have arisen either from seeds or from fallen fruits. All the young plants seen had evidently come from the areolæ of fallen vegetative joints. A search in September 1915 led to the discovery of a dozen rooted fruits which evidently had sprouted during the summer rains. Thus, though fallen fruits readily give rise to new plants in the greenhouse, they apparently do not do this frequently in the field. By following the fruit development of *O. fulgida* through the whole summer it was found that four, or possibly more, generations of fruits may be added to one of its fruit chains in a single growing-season. The primary flower of the season, developed in spring from a persistent fruit of the preceding year, may form secondary flowers from its own areolæ. These secondary flowers open several weeks after the primary ones and may themselves give rise to tertiary flowers, and the latter in turn often form flowers of the fourth generation for the season in August. In other cases only one or two fruits, or sometimes none, are added to a chain during a whole season. Hence it is evident that the longest chains seen, made up of 12 or 14 fruits, may be formed in three or four years or may take eight or ten.

A study of the behavior of the fruits of other species of *Opuntia* growing about Tucson and at Chico, California, showed that there are several species in which the fruits may persist for one or two years attached to the parent plant, though none forms such large fruit-clusters as *O. fulgida*. Thus in *O. spinosior*, *O. arbuscula*, and in certain plants of *O. versicolor*, at Tucson, many single, persistent normal fruits and occasionally chains of two or three were found in April. In several of the flat-jointed opuntias about Tucson and in most plants of *O. versicolor* no attached fruits were found in April 1915 except abnormal ones that harbored the pupæ of the cactus fly, *Asphondylia opuntia*. Most of these galls had the form of hypertrophied, unopened flower-buds. In these the red of the petals still persisted and, aside from being twice the normal size, they appeared as if just ready to open. They do not open, however, but in May the pupa-cases protrude through the wall of the fruit, the flies escape, and by June most of the galls have withered and dropped. A few only of the less hypertrophied buds formed flower-buds from their areolæ in 1915. In only two or three instances had a persistent gall given rise to a vegetative joint. When these galls of *O. versicolor* were planted beside the fruits of *O. fulgida* on soil in the greenhouse, they did not, like the latter, give rise to vegetative shoots, but withered and decayed.

The development of vegetative shoots from an attached fruit is as rare in *Opuntia fulgida* as in *O. versicolor*, only two cases having been seen in hundreds of plants examined. In *Opuntia arbuscula*, however, the lower of the attached fruits of certain plants regularly give rise to condensed vegetative shoots of several internodes each. When these fruits are put on damp soil the condensed shoots push out to initiate new plants. Attempts to artificially produce this vegetative proliferation of the areolæ of attached fruits of *Opuntia fulgida*, by removing all but three of the fruits of a cluster of 150, failed. In all the experimental plants thus far examined the few fruits left gave rise to flowers only, just as the fruits of the undisturbed clusters do.

The flowers of *Carnegiea gigantea* show certain irregularities in distribution and rate of development. These irregularities were studied by the aid of a compass in scores of crowns in the field and were accurately plotted for a number of typical crowns taken into the laboratory. The flowers were found to be either far more numerous on the east side of the stem, or, if more equally distributed, the flowers of the east side are more advanced in development. This one-sided growth is, perhaps, dependent on the higher average temperature of the east side of the thick stem, due to the fact that this side is not only first warmed by the sun in the morning, but also retains its temperature till late in the afternoon because of the relatively high temperature of the air from mid-day till sundown.

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PERSONS ENGAGED IN VARIOUS ACTIVITIES WITHIN THE YEAR
NOVEMBER 1, 1914, TO OCTOBER 31, 1915.

Scientific Staff:

William A. Cannon; Daniel T. MacDougal; Forrest Shreve; H. A. Spoehr; G. Sykes.

Names of Associates with Subject and Place of Research:

A. L. Bakke. Transpiration. Desert Laboratory, Iowa State University.

N. L. Britton. The Cactaceæ. New York Botanical Garden.

E. S. Clements. Plant successions. Desert Laboratory, Coastal Laboratory.

E. E. Free. Physics of soils. Desert Laboratory.

Ellsworth Huntington. Climatic Change. Yale University.

D. S. Johnson. Morphology of Cactaceæ. Desert Laboratory, Johns Hopkins University, South Harpswell, Maine.

J. C. Jones. Calcium deposits of Salton Sea. University of Nevada.

B. E. Livingston. Moisture relations of plants. Johns Hopkins University, Desert Laboratory.

Francis E. Lloyd. Action of introduced compounds on embryo-sacs. McGill University, Coastal Laboratory.

E. R. Long. End effects of desiccation and respiration. Desert Laboratory.

W. B. MacCallum. The genetic analysis of Guayule. San Diego.

H. M. Richards. Respiration. Columbia University.

J. N. Rose. The Cactaceæ. Smithsonian Institution, New York Botanical Garden.

Edith B. Shreve. Transpiration and movements of desert plants. Desert Laboratory.

J. G. Sinclair. Environic reactions of beetles. Desert Laboratory.

W. L. Tower. Environic reactions of beetles and insects. University of Chicago, Desert Laboratory.

A. E. Vinson. Composition of Salton water. University of Arizona.

Assistants:

B. R. Bovee, J. Dutra, Mary E. Eaton, H. W. Estill, W. R. Fitch, E. S. Johnston, J. C. Strickland, Paul G. Russell.

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