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## NOTICES OF WORK ON FOREIGN VEGETATION

## DESERT ECOLOGY IN NORTH AMERICA AND NORTH AFRICA

- (I) **MacDougal, D. T.** "Annual Report of the Director, Department of Botanical Research." *Year Book Carnegie Inst. Washington*, **12**, 1913, pp. 57—88.
- (II) **Shreve, F.** "Rainfall as a determinant of soil moisture." *Plant World*, **17**, 1914, pp. 9—26.
- (III) **Shreve, Edith B.** "The daily march of transpiration in a desert perennial." *Carnegie Inst. Wash. Publ.*, **194**, 1914, 64 pages, 1 plate, 27 figures.
- (IV) **MacDougal, D. T., and Collaborators.** "The Salton Sea: a study of the geography, the geology, the floristics, and the ecology of a desert basin." *Ibid.*, **193**, 1914, 182 pages, 32 plates.
- (V) **Cannon, W. A.** "Botanical features of the Algerian Sahara." *Ibid.*, **178**, 1913, 81 pages, 36 plates.
- (VI) **MacDougal, D. T.** "From the Red Sea to the Nile." *Plant World*, **16**, 1913, pp. 243—255.
- (VII) **MacDougal, D. T.** "The deserts of western Egypt." *Ibid.*, **16**, 1913, pp. 291—303.

The publications cited above represent a small part of the more recent investigations on desert ecology by the workers at the famous Desert Laboratory, Tucson, Arizona. The establishment of the Laboratory was authorised by the Trustees of the Carnegie Institution of Washington in 1902, the site at Tucson was chosen by F. V. Coville and D. T. MacDougal in 1903, and after local landowners had contributed 200 acres of land and other concessions a laboratory was erected, and W. A. Cannon as Resident Investigator began work in September 1903. In 1905 the Department of Botanical Research was created and D. T. MacDougal appointed as Director with headquarters at the Desert Laboratory. Since then the equipment has been extended to include a Coastal Laboratory at Carmel, California, and experimental plantations at various other places.

(I) This general report on the work done during 1913 contains, like its predecessors, summaries of results obtained by workers at the Desert Laboratory, with many other matters of interest. These reports are indispensable for those wishing to keep in touch with the work of the Laboratory, and instead of attempting to analyse the contents of this condensed report we shall merely reproduce some passages in the Director's introductions to the reports for the last three years, as indicating the breadth of view and the thoroughness which animate the work at Tucson and go far to explain the fine results already obtained by the workers there. "Progress has been made in the attainment of experimental results concerning environic response and physical relations of plants and animals, in the determination and calibration of photosynthetic and other photochemical

activities of green plants, in the co-ordination of data which establish some major conclusions as to climatological history during recent time, and in the accomplishment of systematic observations which yield conclusions of importance as to the origin and fate of plant populations in the course of such climatic alterations." "Progress in modern botanical science necessitates the correlation of a wide range of phenomena interlocking with the activities of plants, and the development of the main researches that have been taken up by the Department has been much like the building of cantilever bridges, the farther ends of which might come to rest upon piers in chemistry, physics, geology, or geography. The chief problems of the Department have been taken to lie in the domain of phyto-chemistry, in the water relations of plants, and in the environic reactions of organisms. The development of methods and the broader interpretation of the results have extended far into the field of conjunctive science, and have led to the consideration of some physical, biological and meteorological subjects which are not usually included within the province of botany but which are of the greatest importance in the geographical aspects of the subject." "Additional results on the relation of plants to climatic complexes secured from experimental cultures in the mountain plantation and at the coastal laboratory have given certain data upon which a factorial laboratory may be planned with a high degree of promise as to its efficiency and importance of results, and the next opportunity for increasing the equipment of the Department will be devoted to the organisation of facilities of this character. The main feature of this laboratory will be adequate power for furnishing heat, refrigeration, light, pressure and moisture control under conditions as exactly regulated as those of a bacteriological thermostat in chambers large enough for plants of full size during their entire development; the construction will include such specialities as the substitution of quartz for glass and devices for the calibration of intake and outgo analogous to those necessary in the operation of a respiration calorimeter. These facilities will enable the worker to analyse or totalise the effect of any one of the factors which make up environment and to test the behaviour of organisms with reference to their previous individual experience or genetic history. Definite advance in some of the main problems of plant physiology must await the organisation of such equipment."

(II) The author points out that while in physiological (or ecological) plant geography much good use has been made of annual totals of rain, seasonal distribution of rain, and the correlation of rainfall and evaporation as criteria for explaining the distribution of various types of vegetation—the influence of rainfall upon the distribution and seasonal activities of plants being obviously exerted through its power of replenishing the soil moisture—in more intensive investigations it is desirable to replace the consideration of rainfall, which is indirect in its relation to plants, by a consideration of soil moisture which is direct in this relation; though the general parallelism of rainfall and soil moisture conditions over large areas, and the ready accessibility of rainfall records, contrasted with the scarcity of soil moisture data, will of course continue to be ample justification for giving rainfall a prominent place as a so-called factor in determining plant distribution. His objects in this paper are to present a digest of a short record of desert rainfall, interpreted in terms of its possible effect upon soil moisture; to give data showing the annual march of water content at three depths in a retentive clay soil; to indicate the relative potency which different falls of rain were found to have in renewing the store of soil water; and to estimate the relative efficiencies of various percentages of soil water for the maintenance of plant activity by correlating them with the concurrent rates of aerial evaporation. The data are skilfully marshalled and presented in striking and ingenious diagrams showing (1) the duration at the Desert Laboratory of rainless periods and of periods without rainfall sufficient to affect soil moisture, (2) the incidence

of rainfall and the march of soil moisture, evaporation and the evaporation-soil-moisture ratio. The average annual rainfall at the Desert Laboratory is 37.1 cm.; there are two rainy seasons, that of summer averaging 63 days in length and yielding 54% of the annual rainfall; the average number of rainy days is 61.5 per year, on 46.2 of which the rainfall is less than 6 mm. In 6 years there were 32 days with more than 1.6 cm. of rain, and they yielded 46% of the total rainfall of the 6 years; there have been periods of 140 days without rainfall of sufficient amount (4 mm.) to affect the soil moisture. The march of soil moisture during the year is closely related to the amounts of the significant falls of rain, and the changes of moisture content are conservative at the lower depths (15 and 30 cm.) in the heavy clay soil investigated. The moisture at 3 cm. falls as low as 1%, and that at 30 cm. rises to as much as 32%. The average moisture of the soil from the surface to 30 cm. in the driest weeks of the year is 6.5%, and in the wettest 29%. The weekly rate of atmospheric evaporation ranges from a minimum of 173 c.c. to a maximum of 1084 c.c.—the annual total being nearly 32,000 c.c. in terms of loss from a porous cup atmometer; this is equivalent to a loss of 345 c.c. per sq. cm. from a free water surface. The ratio of evaporation to rainfall is as 9.3 to 1. The ratio of evaporation to soil moisture fluctuates from a minimum amount to a maximum which are in the proportion of 1 to 10. The ratio of evaporation to soil moisture at the foot of the Santa Catalina Mountains is 9.7 times the same ratio for their summit. The annual amplitude of moisture conditions at the Desert Laboratory is therefore as great as that existing in the most arid portion of the year between localities 1600 vertical metres apart.

(III) The authoress begins by pointing out the striking differences with regard to total annual water loss between the various species of perennial plants indigenous to the vicinity of the Desert Laboratory. These perennials fall into two general types, succulent and non-succulent. The latter are again divided into (1) small plants whose perennial parts are confined to roots or underground stems; (2) plants continuously in leaf; (3) tropophytic plants, which drop their leaves more or less quickly in times of drought. *Parkinsonia microphylla* differs from the other tropophytes in having a continuous covering of epidermis over all its parts, even the branches over 100 years old having an active chlorophyll layer covered by an unbroken living epidermis, hence though the tree is leafless during drought it must still lose much water, yet it is apparently a successful desert species, growing abundantly and well on slopes of all exposures. The leaves have minute leaflets; adult trees in natural conditions bear 1 to 8 dead limbs and have 5 to 10% of the medium-sized branches dead; about 30% of the twigs are dead for a distance of 2 to 5 cm. from the ends, and after the first dry season succeeding growth practically all the twigs are dead for a distance of 0.2 to 0.5 cm. from the ends. The leaves appear in the late winter after the rains, are usually shed during the arid fore-summer, reappear within a few days after the summer rains begin, and persist for varying length of time according to the amount of rain during early autumn. With progressive desiccation of air and soil the leaflets drop, leaving the rachises attached, then if no rain comes the rachises are shed, and after a month or so the ends of the twigs die. The leaflets show opening and closing movements; during cool or moist seasons they remain open or partly open during the day, but during the dry spring and autumn seasons they close soon after sunrise and remain so all day.

The first part of this extremely valuable memoir is devoted to transpiration studies, and the much longer second part to studies involving factors correlated with transpiration behaviour—daily course of stomatal movement, of water content of leaves and twigs and stems, of leaf temperature, and of transpiration under conditions of high and low evaporation. Under each of these headings the authoress deals successively with the methods used and the experiments made on seedling plants, on older plants grown in pots and on

branches of adult plants taken from the field ; the results of the experiments are set out in tables and as graphs, and these are followed in each section by a discussion of the subject investigated. Some of the points brought out in the general summary are given below.

The relative transpiration rates of the plants used differ according to the previous environmental history of the plant ; hence conclusions regarding the actual transpirational rates of plants in situ cannot be drawn from the measurement of water losses from potted plants. Different branches of a tree differ in relative transpiration rate no more than do the relative transpiration rates of the same branch on different days, and relative rates of different branches agree as well as do the rates of different potted plants taken on the same day or the rates of the same potted plant on different days ; therefore the transpiration behaviour of an adult tree may be known better from the measurement of small branches than from that of potted plants. The maxima for relative transpiration of potted *Parkinsonia* plants were found to vary directly with the soil moisture, and some evidence was obtained for the same variation in the case of plants in situ. The maxima of relative transpiration varied with the structure of the tissues in the order to be expected from their anatomical structures. The actual transpiration of adult trees and of young seedlings growing in the open shows a maximum which occurs 2 to 3 hours earlier than the maximum of evaporation for the day. This maximum is followed by an abrupt drop and a subsequent rise, the rise being much more pronounced in the case of branches in leaf and being usually great enough to appear as a rise in the relative transpiration. In greenhouse-grown potted plants the early maximum appears in the relative transpiration but not always in the actual transpiration, and a drop appears in various forms ranging from a distinct drop in actual transpiration to only a slight flattening in the slope of the relative transpiration curve. The early maximum does not appear even in the relative rate when readings are taken in the shade. While the curve of stomatal behaviour follows the relative transpiration curve in such a manner that the existence of an interrelation is evident, no conclusions regarding cause and effect can be drawn from the measurements taken. Water content determinations of leafless twigs and branches 1 m. distant from the twigs show an inverse relation, while the curve for the twigs follows the relative transpiration rate. Curves from further determinations of water content of twigs and their leaves show a relation to transpiration and relative transpiration curves, from which is offered the theory that the drop in relative transpiration and in actual transpiration is due to a slight drying-out of the tissues. *Parkinsonia* trees in sunlight show hourly changes in the relative transpiration rate, in the amount of opening of stomata, in water content of leaves and twigs and in leaf temperature, and these have evident interrelations which are held to be governed by the ratio of the demand to the available supply of water.

Since, as is well recognised, the transpiration-absorption water balance is probably the most vital factor governing the occurrence and distribution of plants in desert and semi-desert regions, the facts brought out by the work of the authoress are clearly connected with the success of *Parkinsonia* as a desert perennial. The responses made by the adult tree to the coming on of drought conditions occur in this sequence :— (1) the leaflets begin closing earlier each day until finally they remain open only a few minutes at dawn and at twilight ; (2) the transpiration amount is lessened with the drying out of the soil ; (3) the leaflets drop off, and later the rachises ; (4) the twigs and small branches begin to die until finally, when extreme drought conditions prevail, whole limbs are lost without injury to the vitality of the plant, and thus the tree passes through the drought period despite the large amount of evaporating surface still exposed at the time of the falling of the leaves. Besides these seasonal responses, the tree has a daily response

which consists in a closure of the leaflets, followed several hours later by a lessening of actual transpiration rate, while the evaporating power of the air is still increasing; this decrease is accompanied by closure of the stomata, lowered water content of leaves and twigs, and a slight rise in leaf temperature; the drop is followed by a rise, but in general the maximum transpiration is not again reached for that day. That seedlings do not respond so readily to seasonal changes is to be expected from the size and structure of their leaves, which differ little from those of greenhouse-raised plants; seedlings are frequently found in drought seasons with dead leaves attached, killed outright without falling. Probably the more mesophytic type of leaf cannot endure the "incipient drying" (brought about whenever the ratio of water loss to water supply in the leaves is rendered less than unity) to so great an extent as the more xerophytic type found on the adult trees. The authoress is engaged on a further investigation of the transpiration behaviour of seedlings and adult plants during different seasons of the year, which will doubtless throw more light on the variations of transpiration and root absorption with soil moisture.

(IV) This monograph of the Salton Sea is the most elaborate publication resulting from the work of the Desert Laboratory staff that has yet appeared, and it contains the results of a fine piece of cooperative research carried on since 1907 and still being continued. The volume is almost unique in that it deals with a remarkable series of phenomena, opportunities for the study of which are but rarely presented. The chief interest of the study of the Salton area centres in the fate of organisms overwhelmed by floods, in the physical changes that follow emersion, and in the biological mechanism of reoccupation of sterilised areas as they emerge from the water—episodes which must have been repeated in their main features many times in the history of the earth's surface.

The Cahuilla basin, lying west of the lower (southern) part of the main delta of the Colorado River, has been the scene of alternate submergence and desiccation, which have occurred many times in the last few centuries, as attested by the numerous beach formations and travertine layers on the shores. The present Salton Sea is the residual lake of the ancient Lake Cahuilla formed in Tertiary times when the head of the Gulf of California was cut off by the Colorado delta from the free access of the sea and so became an inland salt or brackish lake, with the river at certain seasons and stages of flood flowing into it. The Salton Sea was formed by the cutting of irrigation canals and the uncontrolled flow of the Colorado water, resulting in a partial flooding of the desert basin. The body of water which threatened the restoration of the former lake conditions had in 1907 attained an area of over 400 square miles, with a maximum depth of 80 feet; it submerged railway stations and necessitated the removal of the Southern Pacific track for 67 miles to a higher bed, but in that year the railway engineers stopped the deluge by diverting the Colorado River to the Gulf, and the gradual disappearance of the Salton Sea by evaporation commenced, and is still in progress. It was estimated at that time that the Sea would practically dry up by evaporation in about 18 years, and observations have shown that since 1907 the actual evaporation has been almost exactly at the rate of 5 feet per annum.

Following descriptions of the geography and geology of the basin and of its soils, analyses are given of the Salton water, and the remainder of the volume (pp. 49–182) is devoted to the biological results obtained by the different investigators who have collaborated with Dr MacDougal. The annual increase in concentration of the water has been fairly uniform since 1906, and the proportion of total solids has now risen to a little over 1%. In his account of the micro-organisms of the Salton Sea, Prof. Peirce remarks upon the surprisingly large and increasing number of plant and animal organisms which live under what are commonly supposed to be fatal conditions, and he points out that while in the case of moulds which thrive on solutions of strychnine, formalin, carbolic

acid, etc., and the insects in oil-wells and asphaltum, conditions are fairly uniform, it is harder to understand how organisms like the brine shrimps (*Artemia*) and the lowly flagellate, algal and protozoan forms found in the Salton Sea and other strong brines (*Dunaliella*, *Pyramimonas*, *Carteria*, etc.) can exist under conditions ranging from rain-diluted sea-water to concentrated brine from which common salt crystallises out, and even survive enclosure in the salt crystals. The artemias and protozoa feed mainly on two species of *Dunaliella* and various bacteria, and interesting details are given regarding the life-history of these organisms and the conditions under which they live. The bacteria are dealt with partly by Peirce, who describes the specialised brine-inhabiting putrefactive forms, of which one at least is chromogenic, giving a red colour to the brine itself, while M. A. Brannon in his study of the action of micro-organisms on the tissues of woody plants submerged by the flooding of the Sea, notes that the destruction of these is effected mainly by bacteria of the *Amylobacter* group. J. C. Jones contributes a section dealing with the part played by *Calothrix* and other algae in the formation of tufa deposits.

In the next chapter S. B. Parish gives an account of the vegetation of the area lying between the margin of the prehistoric Lake Cahuilla and that of the present Salton Sea. He distinguishes five "formations"—hydrophytic, helophytic, halophytic, mesophytic and xerophytic. The extreme paucity of the hydrophytic flora is attributed to the waters of the streams and canals being so heavily loaded with silt as to prevent the growth of aquatic plants, and the amount of clear water being very limited; in fact, only in one place was a submerged vascular plant seen, the bed of a shallow stream being filled with *Ruppia maritima*. In the helophytic series two associations are distinguished—that of springs at the upper (northern) end of the Salton Sink with *Typha latifolia* and *Scirpus olneyi*, and that of the rivers and canals at the lower (southern) end with *Typha latifolia*, *Scirpus paludosus* and *Cyperus erythrorhizos*. In the halophytic associations, which are much more extensive and cover large areas of the alkaline mud flats, the dominant plants are almost everywhere chenopods; parts where the alkaline content exceeds the amount tolerated by the otherwise almost ubiquitous *Atriplex* spp. are occupied mainly by species of *Suaeda* and *Spirostachys*. As might be expected from the climatic conditions and the desert character of the surrounding country, mesophytes are poorly represented and are more or less xerophytic in facies; they are mainly *Populus macdougalii*, *Salix* spp. and *Baccharis glutinosa*, all small- or narrow-leaved forms. The xerophytic vegetation is a part of the general flora of the Colorado desert, differentiated mainly by the great preponderance of species of *Atriplex*, and this formation occupies an area exceeding the combined areas of all the others, comprising the greater part of the basin. It is remarkably uniform, though showing three associations depending upon the nature of the soils and distinguished as the associations of the detrital slopes, of the clays, and of the mounds of loose drifted materials found in different parts of the basin. The total flora of the Salton Sink consists of 202 species, of which 179 are seed-plants. Of the 79 xerophytes found, 51 are common in some parts of the basin and 2 are abundant everywhere in the arid soils and the alkaline soils—these species, *Atriplex canescens* and *Isocoma veneta*, probably equal in number of individuals the united total of all the other plants above the rank of herbs. There are 6 endemic species of seed-plants in the Sink.

In the largest section of the book (pp. 115—172) Dr MacDougal brings together the various features outlined by his collaborators and presents an admirably clear picture of the movements of vegetation in this desert basin as indicated by the history of the strands or zones emerged during each year of the recession of the Salton Sea since the Tucson workers began their observations. This history may be summarised as follows. (1) The lake rose quickly to its maximum level and also receded quickly. (2) The infiltration and leaching of the soil varied year by year according to the influence of the concentration

of the water on one hand and the time of submergence on the other. (3) The salt content of the water, least in 1907, increased by 18 to 20‰ in each succeeding year. (4) Each emerged strand would therefore be saturated with a soil solution resulting from the infiltration of lake water of the concentration and composition prevailing in the period preceding emergence. (5) The desiccation of the emerged strands would proceed at a rate determined by the character of the soil and by the composition of the infiltrated water. (6) The rising water of the lake picked up seeds lying on the surface of the strands, and the survival of these seeds constituted a means of revegetation, especially of the strand bared in 1907. (7) The rates of evaporation and recession of the lake varied with the seasons, the total evaporation being estimated at 116 inches per annum while the average annual rainfall was 2.74 inches. (8) Rapid recession of the water would result in separating stranded seeds quickly from the margin of the water and in setting up rapid desiccation of the surface layer of soil, which would be unfavourable to germination and survival. (9) The shallow water lying on mud flats fringing the shores was raised to a much higher temperature, 15° to 20° F., than the body of the lake, even during the winter, thereby greatly increasing its toxicity for seeds, seedlings and propagative bodies generally, and most of the seeds falling into the lake would be subject to this toxic action, hence the muddy flats fringing the shores at all stages of the lake's history would form a barrier that would be crossed by a plant carried out into the lake and again when deposited on a beach. Details are given of the invasion and revegetation of the strands formed from 1907 onwards, and the behaviour of the invading plants, most of which were carried as seeds by the wind or by flotation or by birds. Other topics dealt with in this interesting chapter are the influence of the lake on the vegetation of the dry slopes above its level, the endurance and survival of seeds and plants, the biological and physical conditions of dissemination and reoccupation, the flotation and germination of seeds, the processes of succession and elimination, and the reoccupation of emerging sterilised islands (see Plate V).

(V) The author gives a result of a tour in southern Algeria in the autumn of 1910 and the spring of 1911, the distance covered in the more arid portions being about 1000 miles. The most important topographical features of northern Algeria are the mountain masses constituting the Atlas range, lowest in Tunis, highest in Morocco and reaching in Algeria itself intermediate heights of about 2200 m. In the east they constitute a single general uplift though made up of several groups, but westward the mountains separate into a northern range (Tellian Atlas) and a southern range (Saharan Atlas). Between the two ranges lies a region of steppes, the High Plateau (average altitude about 1000 m.), which has a monotonous topography, with gently rolling surface and here and there undrained depressions (chotts) where salts accumulate—in rainy seasons the chotts contain water, in the arid summers they are dry. South of the Saharan Atlas lies the desert, comprising about 2,000,000 square miles and showing extremely varied topography. In the extreme southern portion of the Algerian Sahara, crossed by the Tropic, there is an extensive highland, the plateau of Idghagh, reaching an elevation of over 1500 m.; all of the Sahara to the west of this plateau is above sea-level, much of it having an altitude of over 300 m. North from the Idghagh plateau the country gradually descends to the depression of which the great Chott Melghir is a part, a region below sea-level; here extends also one of the longest oueds of the Sahara, the Oued Igharghar, which rises in the Idghagh plateau and empties in the Chott Melghir, its entire length exceeding 700 miles. The oueds are valleys resembling the arroyos of the southwestern United States, in that they carry water for a small portion of the year only, when the torrential rains fill them with a muddy flood.

The topography of the part of southern Algeria specially dealt with in this work



(lying between Laghouat and Ghardaia, between Ghardaia and Ouargla, and between Ouargla and Biskra, all to the south of the Saharan Atlas) is probably representative of much of the rest of the Great Desert. Laghouat, about 800 m. high, lies on the northern edge of the region of the *dayas*, a region of poor drainage and a slightly undulating surface with frequent depressions, each the centre of an area from which it receives flood-waters. The *dayas* differ from the other undrained areas, the *chotts*, in that they do not contain an excess of salt, owing probably to efficient subdrainage. Between Ghardaia and Ouargla (southeast of Ghardaia) are undulating stony plains (Gantara or Hamada region), large salt spots (*chotts*), and a prominent range of sand mountains (*areg desert*) about 300 m. high. At the eastern edge of the Gantara the general level of the country drops suddenly about 65 m. to the Ouargla plain (*reg desert*) with altitude under 160 m.—this is an eroded flood-plain of the Oued Igharghar or its tributaries. The richest vegetation is found along the oueds and the adjacent flood-plains; here the water relations are the most favourable, and the oueds constitute highways along which plants venture into the desert from the more humid regions.

In certain broad features the physical environment of the plants of southern Algeria is similar to that of the southwestern portion of the United States—these regions have about the same latitude, both are separated from a large sea by mountains, and the range in altitude is similar. These two widely separated regions are, however, very unlike in such features as the amount and distribution of the precipitation, and a correlated difference in the habit and composition of the flora is apparent. Climatically Algeria falls into three main provinces—the Tell or littoral portion between the Tellian (Maritime) Atlas and the Mediterranean, the High Plateau or steppe between the Tellian Atlas and the Saharan Atlas, and the Desert—which differ markedly in rainfall, temperature, and other climatic features. In the Tell and the High Plateau the winds from the sea deposit most of their moisture—along the coast as much as 700 mm. of rain is recorded; on the High Plateau, 310 mm. annual rainfall; in the Desert south of the Saharan Atlas, with lowest altitude and highest temperature, 200 mm. and less—in some years no precipitation whatever is recorded in the desert. The seasonal distribution of the rains in any arid or semi-arid region is an important factor in shaping the character of the vegetation. For example, in the semi-arid Tucson region there are two distinct rainy seasons, in winter and summer, and here plants with a water balance are an important feature, but farther west, where there are no summer rains, there are no succulents. In Algeria, also, there is but one rainy season, and the absence of plants with water-storage facilities is one of the leading characteristics of the vegetation. The percentages of the rainfall for winter, spring, summer and autumn are: Tell, 42, 27, 4, 27; High Plateau, 30, 20, 16, 34; Desert, 37, 39, 4, 20. Hence both in the Tell and on the Desert there is a long dry summer season, but in the intervening country more or less rain falls at this time of year. The mean relative humidity changes markedly as one passes from the Tell, across the High Plateau, and enters the Desert: at Algiers it is 85%; on the desert it varies from 42 to 54% and is often 7 to 9%, or may in midsummer be too low to measure with instruments, though in autumn it becomes surprisingly high owing to lower temperature and the northerly winds. With this great difference between the Tell and the Desert in relative humidity there is associated marked variation in the rate of evaporation: at Algiers the total annual evaporation is 1654 mm., while at Ghardaia it is 5309 mm.—probably the highest amount of evaporation yet recorded. The seasonal evaporation-rainfall ratio for the littoral is 2.5 : 1; that of the Tell is 3.5 : 1; that of the High Plateau is 9.4 : 1; and that of the Desert is 46.5 : 1. The annual temperature variation at Algiers is about 41° C., at Ghardaia 48° C. to 57° C.; the daily variation is especially marked on the High Plateau (about 17° C.) and on the Desert (20° C. or more); the

absolute maximum temperatures are fairly high—about 50° C. at Ouargla; and usually in winter freezing temperatures are experienced at all stations in southern Algeria. In addition to rainfall, evaporation, and temperature, air-currents form an important factor, not easily stated in accurate terms; a calm day is rare on the Desert; the sirocco or desert wind, which crosses the Mediterranean and is felt in southern Europe, blowing chiefly in spring and summer, raises the rate of evaporation and thus increases the arid conditions, while winds from the north bring cooler conditions and lower the relative humidity and evaporation rate.

The effect of a varying amount of precipitation is naturally the most marked climatic factor, and is especially striking as one goes south from the Mediterranean. The leading characteristic of the vegetation of the littoral and of the Atlas Mountains is the presence of forests; with an all-land connection with the European continent in earlier geological times, the flora and fauna of this portion of northern Africa are, as might be expected, closely allied to those of southern Spain, France, and Italy. Along the littoral, at and near Algiers, there is a wealth of native and especially of introduced plants, including many subtropical forms and giving little hint of the arid regions close at hand. The forests of Algeria lie mainly in the Tell, though some species occur in the Saharan Atlas as well; trees also grow along the oueds, especially on the High Plateau, but not in sufficient abundance to form forests proper. The chief conifers are *Pinus halepensis* (sea-level to about 4000 feet), *Cedrus atlantica* (4000–6000 feet), and *Juniperus* spp. (abundant but not forming forests); three oaks—*Quercus suber* (sea-level to 2500 feet), *Q. ballota* (2500–4000 feet) and *Q. lusitanica* (3500–6000 feet)—are forest-forming species, but *Olea*, *Platanus*, *Fraxinus* and *Pistacia* also share in the formation of a mixed forest. As the littoral is left behind the forests disappear, until on the High Plateau there are only straggling trees and shrubs (*Tamarix*, *Zizyphus*, etc.) along the watercourses; the vegetation is sparse, owing in part to the rather low rainfall but largely to lack of efficient drainage, large areas being heavily charged with salts and halophytic plants forming an important element in the flora of this region, while in the most intense salt areas no plants are found at any season. South of the Saharan Atlas a marked change occurs: here, with a rainfall of 200 mm. and less, the trees are confined to the dayas, the vicinity of oueds, and the oases; the shrubs of the hamada decrease in numbers as one goes south, and where the annual precipitation is least, as on the Gantara between Ghardaia and Ouargla, large barren areas extend. Apart from the effects following a lessened annual precipitation there is also to be taken into account the increasing uncertainty of rain, or its irregularity, which is a marked character of the Saharan climate; probably the vegetation of the desert, both as to amount and kind, is determined by the capacity of desert forms to meet successfully occasional, or even rare, adverse conditions of whatever sort.

The environmental conditions encountered by plants in arid regions differ widely from those of moister areas. Precipitation is only slight, but shows an enormous range of variation from year to year; the rate of evaporation is high; the temperature of the air and soil varies widely both during the day and with the seasons; the light is of great intensity; the soil is low in humus content and may contain an excess of salts. These, the most striking physical factors of deserts, are present in different combinations with resultant differences among deserts, and an arid region may be so large as to include much variation within its borders. Again, a desert may be so far from the ocean, or may include such diversity of topography, as to show great variation in biological features as well as in its surface phenomena. In the flora of any arid region the mutual relations of the constituents of the flora and its general and detailed relation to the physical environment are quite different in the main from these features in the flora of the more humid

regions. The chief relation is that to water, and on the response of the plants to this relation depend most of the phenomena associated with desert plant life. In extreme deserts the element of competition between the perennials—an important factor in the survival of a species in the moister regions—is probably entirely absent; though in the less extreme deserts, as in the vicinity of the Desert Laboratory in Arizona, there is competition between plants—in this case competition not for room but for water, and manifested not by palpable crowding but by the less obvious competition of the roots. Thus the reactions are with the physical environment and are exhibited in various ways, some of which concern the plants themselves in an intimate manner, being morphological and physiological, while some are concerned with the flora as a whole. The flora of a desert is in part perennial, lasting with but little outward change from season to season, and in part ephemeral, consisting of short-lived species which appear with the rains and disappear with the return of the dry season. The ephemeral flora differs in no essential respect from the annuals of the moister regions, and the environment to which they are exposed closely resembles that of the annuals of such regions; but the perennial desert flora shows striking departures from the corresponding flora of moister regions, just as the environment to which they are exposed for the greater part of the year is different.

The most obvious features of desert plants are associated with the subaerial portions: the leaves are usually greatly reduced or absent, during the dry seasons at least; spines are often present and the exposed parts are often well covered with hairs; the stomata are sometimes deeply sunken, the cuticle often very heavy, and leaves or stems may be covered with wax; the chlorophyll-bearing cells are arranged with the long axis at right angles to the leaf or stem surface. All or most of these characters are associated with the low humidity of the air. The root-habits also vary and show marked reactions to environment—the widely extending and superficial type of root is confined to plants with water-storage capacity, plants with a dominating tap-root are confined to areas where the soil is deep, while species with generalised roots have a local distribution which may be considered the maximum. The relation of the superficial type of root-system to the distribution of the species is not so apparent as is the case with the other types; since the absorption roots of plants with water balance mostly lie less than 10 cm. below the surface and are thus subject to extreme desiccation for the maximum time (i.e. they are exposed to favourable moisture conditions for the minimum time), the best development of such fleshy species occurs where the rainfall is periodic, occurring twice a year, and they are wanting or sparse where the rainfall is uncertain or occurs but once annually. Owing to the unfavourable character of the rainfall in southern Algeria, plants with a water balance are absent there, just as they are absent from portions of the southwestern United States where the amount or the character of the precipitation is likewise unfavourable. Again, the non-fleshy perennials of the desert may possess a very dense cell-sap, but certain fleshy species, and such desert mesophytes as have been studied in this respect, have no more highly concentrated cell-sap than the ordinary plants of the humid regions. Desert species which under natural conditions and in the dry seasons form extremely dense juices lose this capacity when grown under humid conditions. As shown by Fitting, the shoots of certain desert plants may possess cell-sap so concentrated as to give osmotic pressure as great as 100 atmospheres, whereas in ordinary mesophytes the usual pressure is given as 5 to 11 atmospheres. Though it has not been shown that the cell-sap of the root-hairs is isosmotic with that in the shoot cells, it is assumed that both the shoots and roots of desert plants contain a very dense sap, and it is probable that the highest concentration will be found in those plants with the generalised root-system, since such plants occupy the most arid habitats.

Nowhere is the edaphic factor, or soil relation, more important than in the desert,

where quantity and quality are always important and occasionally even determining factors. This applies not merely to dunes or chotts in particular, but to the soil most commonly found—in south Algeria a clay with more or less sand. So far as the relation of plant to soil refers to the presence or absence of the plant, the problem may be thus stated: given similar kinds of soil and an equal precipitation, areas where within limits there is greatest depth of soil will have the largest number of plants, and areas with light soil covering will have few or no plants. Also, given sufficient soil, the kind of plants present, together with certain root-types, will depend on the soil depth. Excavations on the hamada at various places showed that on formations of this kind the soil was usually less than 50 cm. deep; in the oueds, where a different type of soil occurs, greater soil depth is of course found; on the reg, or alluvial plain, frequently the flood-plain of oueds, the soil conditions are peculiar and the soil is here also deeper (20–30 m. before solid rock is encountered) than on the higher hamada. The special significance lies mainly in the differences in the water relation conditioned by variation in depth. It appears probable that rain showers so slight as not to penetrate over 1 cm. have little or no direct influence on the perennial vegetation (for instance, filamentous rootlets of *Haloxyylon* were not found nearer the surface than 8 cm.), but should there be sufficient moisture in the soil to permit root absorption, provided a slow rate was adequate to replace the transpiration loss, which loss was made lower by a more moist atmosphere, a slight rain would be of great significance even if it did not penetrate to any appreciable depth. On the intensely arid desert such slight modifications of the water relations as the lowering of temperature as winter approaches, causing diminished evaporation or rains, though actually small in amount, may be of large moment to plants; such a condition was observed at Ghardaia, where there had been a drought for over a year, but on the return of the cold season, with a lower evaporation rate, growth was resumed and several plants came into flower—in fact, plants in the arid desert as a general rule renew their various activities whenever rains chance to come, whatever the season. Hence it appears that sufficient moisture persists in the soil to tide perennials over the long drought periods, though not in sufficient amount to permit active growth during the dry seasons.

Apart from the oases, the various plant habitats are in the Algerian Sahara closely associated with soil differences. These habitats are dunes (areg), stony desert (hamada), alluvial desert (reg), the daya, and the flood-plain of the oueds. The soil of the reg, and often that of the oued flood-plain and that of the daya, is fine alluvial and is relatively or actually deep. The hamada has the poorest soil conditions, being underlaid by rock, while large stones and boulders are embedded in the soil or lie on the surface; a modification of the hamada occurs whenever sand is strewn over its surface, even if the sand is only a few centimetres thick, acting as an effectual mulch, increasing the retentive capacity of the soil, and strikingly changing the character of the vegetation. Finally, in the salt spot (chott) gypsum constitutes an important salt. As regards their relative importance the habitats in southern Algeria may be grouped in the following sequence: hamada, dune, oued, flood-plain, reg, daya; the mountains are here left out of account, since in this area they are barren save for crustaceous lichens, though in the central Sahara where the mountains are high, the mountain climate brings about favourable conditions for plant life. The habitat preferences of the plants of southern Algeria are marked, as would be expected from the striking differences in the habitats. On the dunes the grass *Aristida pungens* is the most abundant and widely distributed sand-plant; on these sandy areas occur also species of *Tamarix*, *Euphorbia*, *Ephedra*, *Limoniastrum*, and other plants in smaller numbers. On the oued banks are *Tamarix*, *Nerium oleander*, and near the oases the date palm and

other introduced plants. On the flood-plains are found numerous species, among which are *Peganum harmala*, *Retama retam*, *Ephedra*, *Genista* sp., and *Haloxylon* sp. The typical plants of the dayas are *Pistacia atlantica* and *Zizyphus lotus*, the latter occurring on flood-plains and the reg as well. The chotts have mainly such halophytes as *Anabasis reticulata*, *Halocnemon strobilaceum*, *Salsola* sp., *Limoniastrum*, and others. The flora of the reg is essentially like that of the flood-plains, as might be expected from the relation of the two habitats. The flora of the hamada is peculiar, having the fewest species and the smallest individuals, most of the perennials being under 30 cm. high; the chief forms are species of *Artemisia*, *Teucrium*, *Centaurea*, *Thymelaea*, *Echinops*, *Henophyton* and *Haloxylon*—the last is possibly the most widely distributed, occurring in other habitats as well.

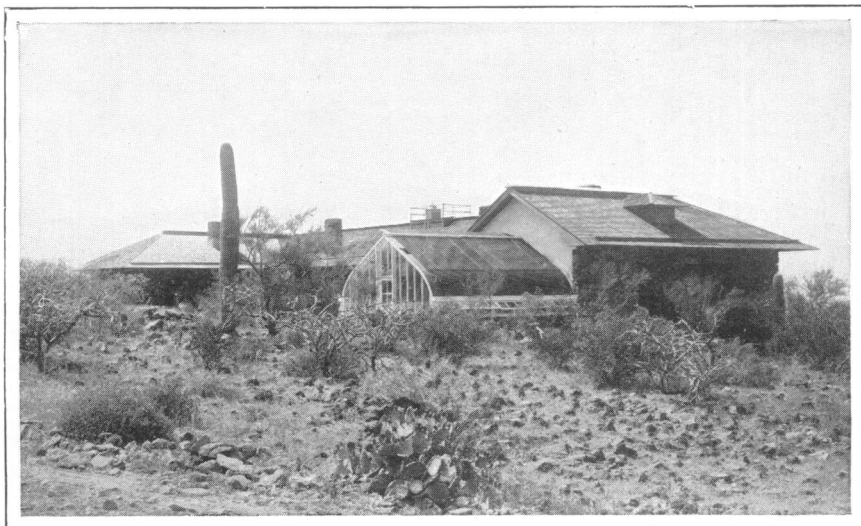
The relation between the type of root-system and the distribution of the species is often, though not always, close and apparent. For example, large perennials, such as *Tamarix* and *Zizyphus*, have an obligate specialised root-system, with a long tap-root; these plants naturally occur where there is considerable depth of soil, and hence are not found on the hamada, for instance, where the soil is shallow. On the other hand, plants with a generalised root-system, like *Haloxylon*, are found on the hamada, but they occur also in other habitats where the soil is deep. The generalised type is flexible, accommodating the species to a wide range of soil conditions, and in doing this the change in form is almost a change in type. For instance, the roots of *Haloxylon* on the hamada develop true laterals and a main root, but in deeper soil the laterals are nearly suppressed and the tap-root is the striking feature. A study of the relation of root-type to distribution in Algerian plants leads to the same general conclusion already obtained by similar but more extended study in the Arizona desert, namely, that the connection is often a very close one and often of definitive importance; where the root-type is an obligate type the distribution of the species is much restricted, but where it undergoes modification with changed environment the distribution is much less confined. The fact that plants occurring where the soil conditions are most arid, i.e. on the hamada or its equivalent, possess the generalised type of root-system affords additional evidence that it is not the most deeply penetrating type of root that is to be regarded as the desert form *par excellence*, but on the contrary it is such a root as can both reach out widely and penetrate as deeply as the soil allows, and in which there is developed a cell-sap of extremely high concentration.

(VI) The opportunity afforded by the journey here described was taken to test the generalisations reached from work done at Tucson on the vegetation of arid regions, with special reference to the light and moisture relations of plants. The author started from Cairo with the object of making a traverse from the Red Sea across the intervening mountain ridge and down the gentler western slope to the Nile, and thence into the Libyan Desert. The journey began in a maritime region with a monsoon climate, where the annual total rainfall (about 23 cm.) is received in midwinter, while the desert—extending almost uninterruptedly westward from the mountains near the Red Sea 3000 miles to the Atlantic—has a continental climate in which the only possible precipitation is that resulting from the upward movement of great volumes of heated air from extensive land masses with consequent inrush of colder air and rainfall. Months or even years may intervene between the coincidences of conditions bringing about precipitation in any one part of this desert, in which the rainfall is so uncertain as to be for the biologist a feature of relatively little importance, the supply for plants and animals being derived from the ground water. The extreme aridity of this North African desert is further indicated by the evaporation that might take place from a free water surface, which is estimated at about 4 m. yearly in parts of the Libyan Desert and

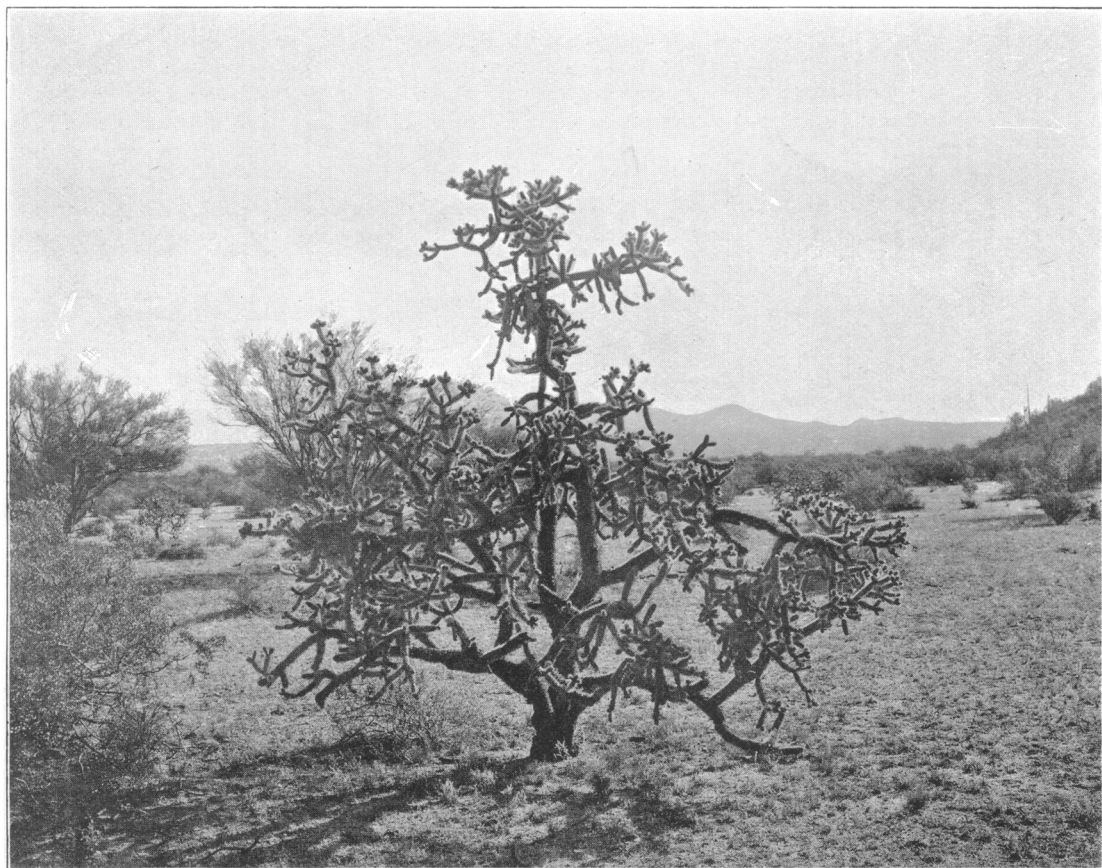
the Sahara to the west, and is much greater than that of any part of the American desert.

A description is given of the vegetation of the shores of the Red Sea, near Port Sudan, which consisted mainly of halophytes with various small herbs and shrubs of the "winter annual" and "winter perennial" types, those not halophytic or xerophytic being of the habit that brings them from seedling to flower in a very short period. On the shore there were large clumps of the succulent *Coralluma*, an Asclepiad genus of which several species were also found extending to the summits of the mountains on the west; this shore form had short main stems dividing into numerous closely arranged angular leafless branches as in the cactus *Cereus*. The slopes of the mountains consisted largely of masses of loose rock material like the "bajadas" of the Arizona cañons, and as the mountains on the Red Sea side rise abruptly from near the sea, the detrital material that had fallen and rolled down the long sloping bajadas had pushed out into the sea. The vegetation of these débris slopes included xerophytic shrubs like *Acacia rubica* and an *Ephedra*-like plant *Leptadenia spartium*, the latter usually found along the margins of dry stream beds. In a stream bed at about 500 m. altitude a rich flora of about 90 species of seed-plants, ferns and liverworts was found, while the steep hillsides bore various leguminous and asclepiad shrubs. On crossing the mountain ridge and starting down the long gentle drainage channels which lead to the Nile, one passes from a flora rich in succulents to a region in which the prevailing types are spiny xerophytes or forms with switch-like branches—succulents not being conspicuous in a climate in which the rainfall is uncertain in occurrence. These wide arid westerly slopes extend to the Nile with its fertile green fringe a few hundred metres or a few miles wide; in places the striking picture was presented of the alluvial lands being all on the eastern shore of the river, while on the west bank the Libyan sands pour over the rocks and down through the narrow screen of shrubs into the river itself, so that one may walk from the Nile into the driest desert in a dozen paces.

(VII) The traverse from the Red Sea to Atbara on the east bank of the Nile (see preceding paper), through a diversified arid region with definitely recurring periodic rainfall, was followed by a visit to a portion of the interior (Libyan) desert, for which purpose the Nile was left near Luxor and a month was spent in the desert, the oases of Kharga and Dakhla being visited. This region has no elevations of any great mass or height, and being far from the sea the rise of heated air and consequent replacement by winds is not followed by rains sufficient to form a factor in maintaining the soil moisture at a proportion sufficient for vegetation; though occasional storms causing precipitation in any one place once in a few or in several years might supply enough moisture to start rapidly growing and short-lived plants, such "summer annuals" were very rare in the region visited. It is the ground water that must be taken into consideration in a study of the vegetation. The oases, which lie mostly in the lowest parts of great basins in the sandstone and limestone where wells and springs occur, are fully occupied and cultivated by man, and their vegetation is of minor interest in the study of arid regions. At various other places however the ground water comes to the surface layers to an extent not allowing of agriculture; these, with sand dunes and rock crevices, are the habitats of the undisturbed native plants. Whereas 172 species were found in the few days devoted to the eastern desert with its diversified topography, varied habitat conditions and definitely recurring rainfall—conditions recalling those of the arid regions of southwestern America—only 13 species were found in the month of wandering over the Libyan Desert in places unaffected by irrigation or agricultural operations, and one of them was a parasite (*Cistanche lutea*) living on the roots of one or more of the other 12! Notes are given on the habits of this "notable dozen," which includes *Alhagi maurorum*,

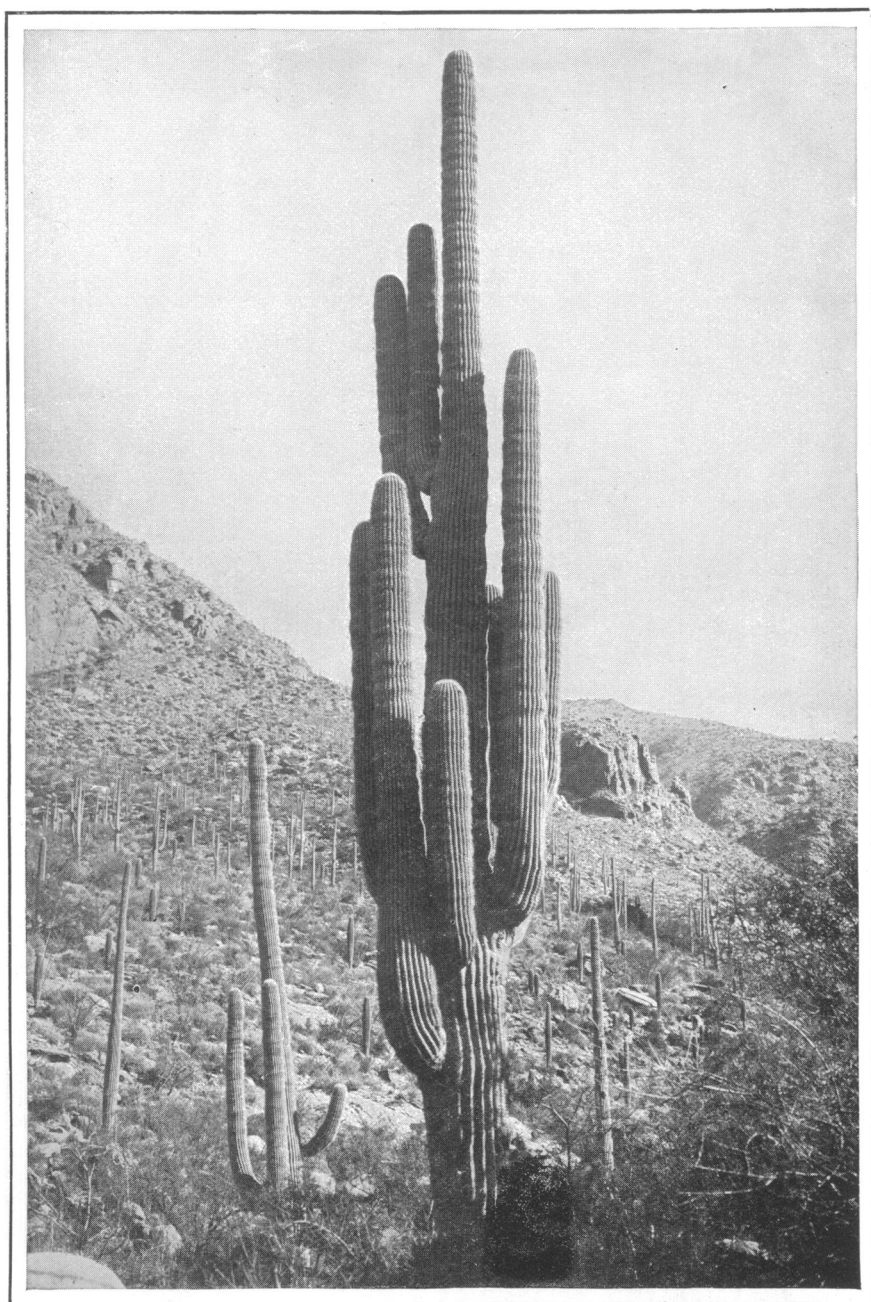


The Desert Laboratory, Tucson, Arizona.



A characteristic landscape in the vicinity of Tucson, Arizona, with *Opuntia spinosior* and *Parkinsonia microphylla*.

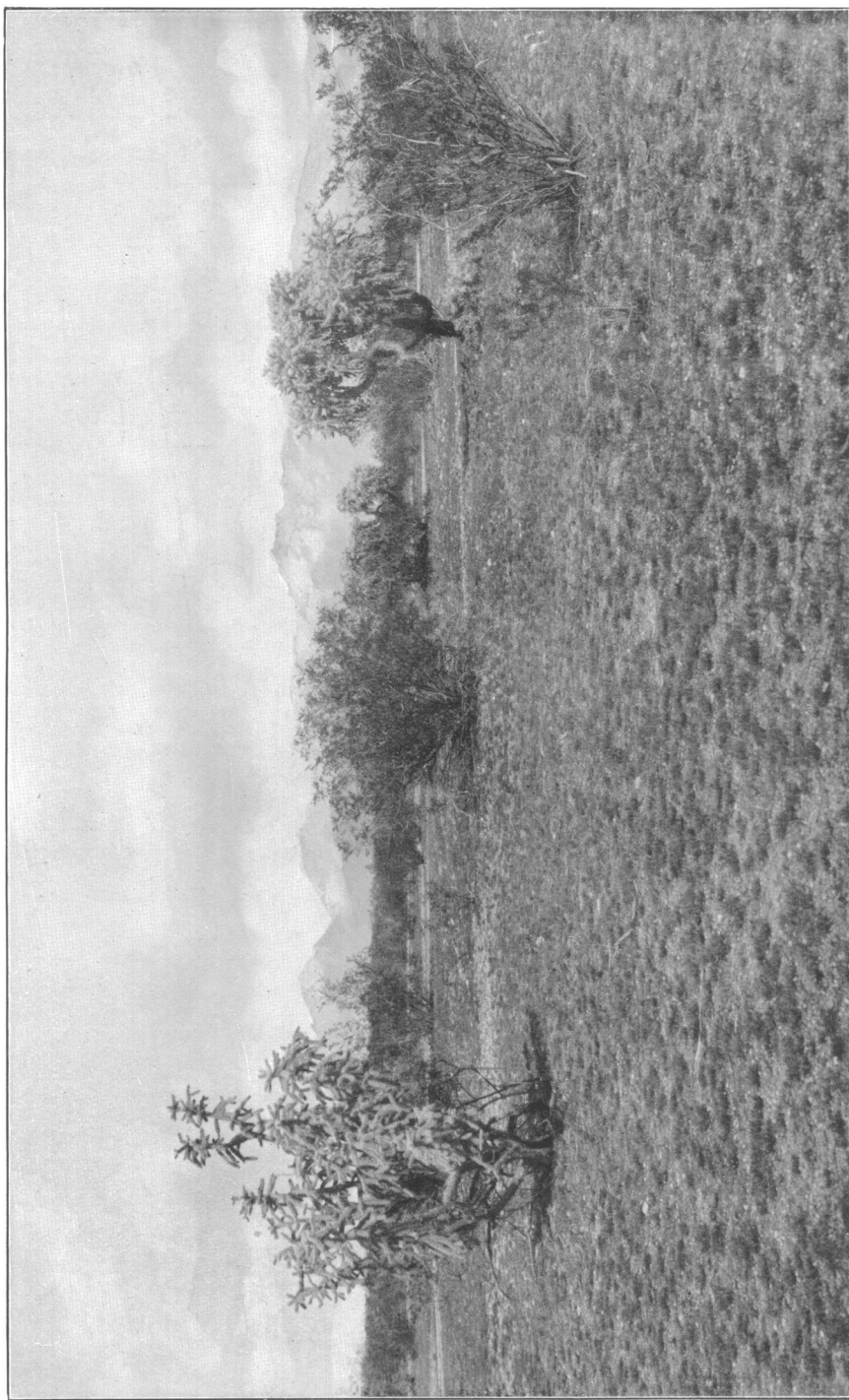
DESERT ECOLOGY IN NORTH AMERICA AND NORTH AFRICA (see pp. 42—55).



*Cereus giganteus* (*Carnegiea gigantea*) in the foothills of the Santa Catalina Mountains, near Tucson, Arizona.

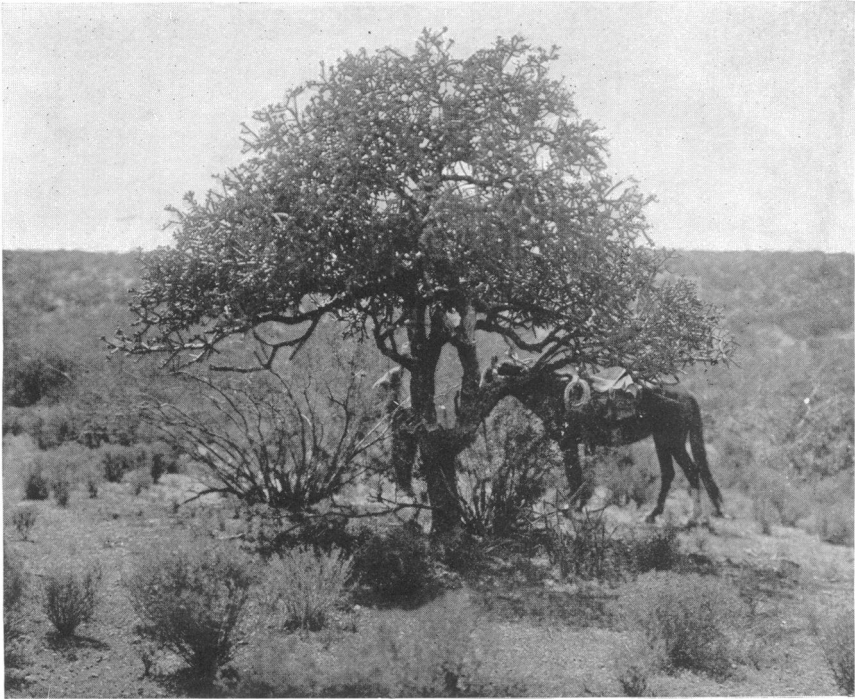
DESERT ECOLOGY IN NORTH AMERICA AND NORTH AFRICA (see pp. 42—55).





Desert landscape in the vicinity of Tucson, Arizona, looking toward the Santa Catalina mountains. *Cercillea glutinosa*, *Opuntia spinosior* and *O. fulgida*. The ground is covered with a late winter growth of herbaceous ephemerals, chiefly *Plantago ignota*.

DESERT ECOLOGY IN NORTH AMERICA AND NORTH AFRICA (see pp. 42—55).



*Opuntia versicolor*, an arborescent *Cylindropuntia*, near Tucson, Arizona.

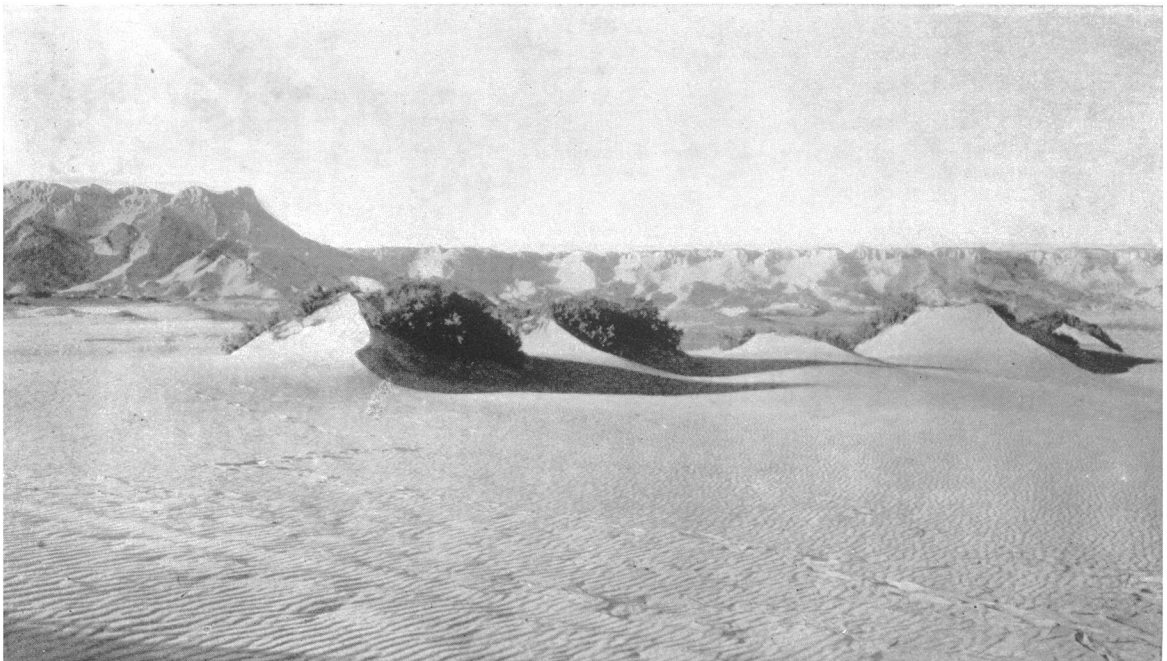


A rocky island in the Salton Sea, southern California, formerly submerged, and now exposed by the recession of the lake. The plant is *Pluchea sericea*.

DESERT ECOLOGY IN NORTH AMERICA AND NORTH AFRICA (see pp. 42—55).

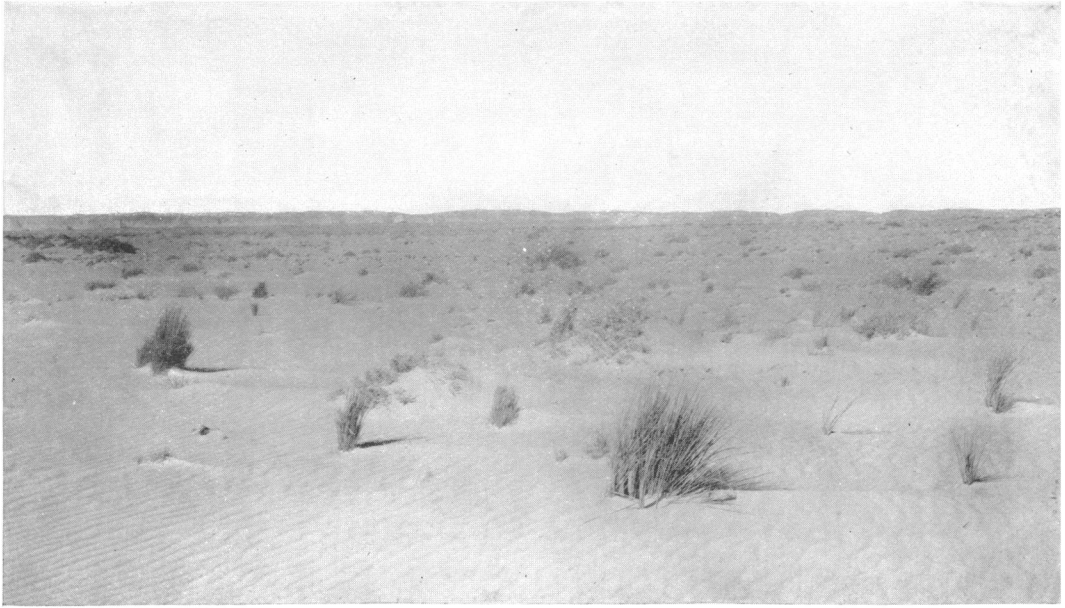


*Agave Schottii*, a succulent characteristic of the chaparral region of the desert mountain ranges in south-western North America.



Accretion dunes around the stems of *Tamarix* in the northern portion of the Oasis of Dahkla, western Egypt. The sandstone escarpment shows erosion by wind.

DESERT ECOLOGY IN NORTH AMERICA AND NORTH AFRICA (see pp. 42—55).



Desert of western Egypt; *Aristida plumosa* and *Calligonum comosum* near caravan track from Farafra to Baharia.



The Oasis of Dahkla in the desert of western Egypt; *Acacia* in the foreground, a sandstone escarpment in the distance.

DESERT ECOLOGY IN NORTH AMERICA AND NORTH AFRICA (see pp. 42—55).



## *Desert Ecology in North America and North Africa* 55

a much-branched spiny shrub 1—1·5 m. high, widely distributed in northern Africa in sandy and gravelly places, and forming a valuable food for camels despite its sharp spines, which are fairly rigid and 2 cm. long; *Aristida plumosa*, a grass abundant in sandy wastes which collects sand by the action of the wind against its clumps; *Calligonum comosum*, a shrub about 1 m. high; *Caryoxylon* (*Salsola*) *foetidum*, a shrubby perennial about 1 m. high; *Farsetia aegyptica*, a shrubby Crucifer with narrow linear leaves; *Haloxylon schweinfurthii*, a small shrub branching from the base, with thick jointed branches; *Imperata cylindrica*, the tall “halfa grass” of northern Africa; *Tamarix mannifera*, a small tree growing in sandy places and capable of enduring highly concentrated soil solutions, stems usually serving as accretion centres for dune formation; *Traganum nudatum*, a Chenopod shrub sharing with *Haloxylon* the character of being found in the most arid parts of sandy wastes and dry slopes; *Zygophyllum coccinea*, a shrub about 1 m. high; a small unrecognised fruiting Leguminous shrub; and an unrecognised annual, probably a Crucifer. While *Alhagi* is spiny and *Aristida* has cylindrical rolled-up leaves, the remaining species are simply indurated and leathery, showing hardly any of the structures to which a protective function is usually assigned; the 3 Chenopods are halophytic, but not succulent enough to permit the accumulation of any great surplus or water-balance. All but one of the species have a wide distribution, spreading over northern Africa and into Asia Minor, and some into the drier regions of India. The author notes that considerable areas were traversed which appeared to be absolutely without vegetation, and concludes that the lack of vegetation in such places is not ultimately due to lack of water but to wind action, since plants were found in places where the water supply was no greater than that of the bare areas. In exposed places the surface layers of sand and gravel are shifted about, exercising a corrosive action that is destructive of plants; highly specialised desert species might survive the aridity, but the shifting substratum does not permit them to attain maturity, a condition which would affect both the tender rapidly developing annuals and the slowly growing leathery xerophytes.

We are indebted to the kindness of Dr Forrest Shreve, Editor of *The Plant World*, for the use of the photographs reproduced in the accompanying plates (Plates II—VII) illustrating the vegetation of the North American and North African desert regions which have formed the scene of the brilliant investigations of the workers connected with the Desert Laboratory.