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GENERAL AND PHYSIOLOGICAL FEATURES OF THE
VEGETATION OF THE MORE ARID PORTIONS
OF SOUTHERN AFRICA, WITH NOTES ON
THE CLIMATIC ENVIRONMENT

BY
WILLIAM AUSTIN CANNON

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VEGETATION OF THE MORE ARID PORTIONS
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INTRODUCTION.

The remarkable vegetation of Southern Africa has received the attention of many scientists and the leading characteristics have long been known. But many features of the flora remain for investigation. Undescribed species are being found. The origin of the vegetation as a whole and that of prominent plant types is being sought. Habitats are being defined and possible relation of species to physical environmental factors subjected to observational and experimental investigation. All of this is at present being done both by individuals working intensively on local problems and in a larger way by the Union of South Africa through the agency of the Botanical Survey, an organization which is pushing forward investigations on subjects possibly not always best suited to separate and individual effort. Such division of labor makes it possible for the visiting botanist to make his contribution without duplicating work already at hand and with hope of contributing to the general end desirable of attainment. So far as the point of view of the writer of these pages is concerned, it was not so much to contribute to the knowledge of the plants *per se* as to measure the conditions of plant life and the characteristics of the plants of the more arid portions of the country with the yardstick of his experiences in other arid lands that led to the visit to the Union.

A botanist, seeing some of the different arid or desert regions of the world, is struck with the obvious differences in the habit of the vegetation, as well as by the differences in the habitats, although he may be quite well aware that there may also be certain features of both which widely separated arid regions may hold in common. He is very likely to be convinced finally that the association of habit and habitat is casual and to a degree local, but that the more remote analogies are casual and depend, to a large degree but not wholly, on the reaction of plants to an environment which may either be like or unlike another environment with which it is compared. That the arid region vegetation of distinct world areas with similar or nearly similar climatic characteristics should ever develop along unlike lines is a matter for investigation.

Although, as suggested, the rainfall of widely separated arid regions may possibly be the same, it does not in the least follow that there is to the same extent a parallel in the vegetation. For example, in the arid desert regions of central Australia, especially in northern South Australia, one encounters shrubs and trees with leaves and leaf-like phyllodia of a leathery texture, which are usually of a small size and not deciduous. There are practically no succulents. In regions with a small rainfall in southern Algeria there are also no or few succulents, but both deciduous and evergreen species occur. In the drier portions of North America are to be found both deciduous and evergreen shrubs or trees and succulents as well. And, finally, in southern Africa there is a great variety of stem and leaf succulents, and of both evergreen and deciduous trees and shrubs growing under arid conditions. Apparently the absence of one type of plant from any given arid region does not necessarily signify that it will not survive there if brought in, as the disastrous results following the introduction of cacti into Queensland would indicate. Also, it is of interest to note that the species of *Acacia* in Australia are evergreen, while in southern Africa, in southern Algeria, and in North America the acacias are wholly deciduous. As between central Australia and southern Algeria the rainfall which is periodic occurs mainly in the cool season, while in the two other regions referred to where species of the genus are to be found the rainfall may be either in winter or in summer, or both in winter and summer. The cause of leaf fall, or of leaf retention, as the case may be, is clearly not always directly traceable in all of the regions to the same characteristic of the precipitation.

In one respect, if not in many, there is agreement in the direction of the development of perennial woody plants in these different arid regions. The species are relatively small, or at least the surface is often greatly reduced. Leaves may be wanting wholly, or they may be present in juvenile stages only, or at any rate they usually are narrow and usually short, and not greatly dissected. Such conditions appear to be traceable to the immediate effect of the desiccating power of the atmosphere as well as to the effects of intense insolation, and such environmental factors are present in all arid regions. But the species may be unlike as regards reactions to such environmental conditions. Some, for example, have the power of giving off watery vapor much more highly developed than other species and appear not to be able to decrease the rate of water-loss when the supply falls below the demand, and when not to do so may mean wilting and ultimate death.

In all arid regions also there is great variation in the temperature as between day and night and from season to season. This is due to the small amount of moisture present in the atmosphere, which permits rapid loss of heat at night.

Having given different species with unlike characteristics of shoot and root already developed, it is not difficult to understand how they may be affected in an unlike manner by great variations of the temperature of the air, by intense insolation, and by low relative humidity. Where the transpiration surface is small, other things being equal, the loss of water will not be large, but owing to the necessity of the manufacture of foods on the part of the shoot, the chlorophyll-bearing organs must still retain a certain expanse for the proper carrying on of this function. Where, however, the light is intense this can be relatively small. Various devices may be found to occur in plants of arid regions, aside from the reduction in the surface, by which the same ends are attained; that is, immunity from injury from excessive desiccation and excessive solar radiation, while at the same time photosynthetic activities can proceed. But such modifications affect directly the relation of the shoot to temperature as well. In the case of xerophytes of arid regions, where the transpiration is not large, the cooling is largely by radiation only and the shoots, particularly those with water-balance, may become excessively warm.

The three environmental factors above mentioned directly affect the shoot, but only the general moisture relations and the great temperature changes of the air directly affect the roots, and then mainly through the medium of the soil in which they are placed. Roots of different character, as whether fleshy or fibrous, sparse or copious, deeply placed or superficially so, are affected in an unlike manner by these atmospheric factors in a way quite analogous to the shoot. Unlike the shoot, however, there apparently is no "xerophytic" type of root-system, unless the meager and usually shallowly placed roots of most succulents, and at the other extreme the deeply penetrating roots of species where there is sufficient soil and an accessible water-table, or at least deeply penetrating water, can be said to be such. And aside from the roots of succulents, including root succulents, those of species growing in analogous habitats in widely separated arid regions probably closely resemble one another, and possibly do not exhibit differences attributable to or associated with the region of which they are native, in a way or to a degree at all analogous to the behavior of the shoot.

Organs or structures peculiar to plants of extremely arid regions, as compared to species of semi-arid regions, for example, are doubtful. The presence of trichomes, the reduction of the transpiring surface, the orientation of the leaves, double epidermis, heavy outer cell-walls of the epidermis or its cuticularization, mucilaginous cells, as well as the in-rolling of leaves, and the great development of cell-wall material, are not confined to species of the most arid regions, but in them may find the most complete expression. This general type of development, however, which is probably to be regarded as an expression of the

reaction of the plant to some features of the moisture and light environment, more especially, may be so highly specialized as almost to constitute special structural form. Of these might be mentioned the very great, almost exaggerated, cell-wall development in many Australian sclerophylls, as well as the curious development from secretions in *Hakea* of a supra-epidermis with continuous air-cavity between it and the true epidermis, and provided with pores. The true stomata open into the cavity and thus are only indirectly connected with the atmospheric air.¹

Although thus there may be no break in the continuity of structures as between species inhabiting extremely arid regions, and those in regions better favored with rain, with the effect that there is no type which is peculiarly eremologous, there is, however, a special class of plants which are indigenous to regions of moderate rainfall, but which may extend to a certain degree both into regions of smaller and of larger precipitation. Such are succulents, or species having the capacity of storing water, occasionally in large amount, because of the organization of cells containing mucilaginous material. An apparent characteristic of all succulents is the meager development of the roots. Moreover, it appears that the roots of succulents are usually placed near the surface of the ground and do not penetrate deeply, irrespective of its depth. The destructive effect of a sudden excess of water, whereby cells may be ruptured, is not unknown in species of this type. Under natural conditions, possibly as a consequence of these factors, succulents do not inhabit extremely moist soils, but, on the other hand, may be situated in soils which are subject to periodic drying and those which may be shallow. The suggestion seems pertinent, although put forward tentatively, that the type of root development of succulents, the usual situation of succulents with respect to depth of soil and its moisture content, including the depth to the water-table or otherwise perennially wet soil, and their presence in regions having periodic rainfall, are all dependent on the presence of mucilages in the cells of such plants. An extensive root system with possibility of correspondingly large capacity for the absorption of water, or the placing of the roots so that such large absorption is especially forwarded, or a large and continuous supply of water, might operate to disorganize the tissue as above suggested. It is of interest to note in this connection that such harmful effects are averted in certain cacti by the organization of leaves having great transpiring power at the time of the most intense vegetative activity and when the capacity for water absorption is particularly large.²

The present study is the third of a series, in the writer's minor research, of occasional papers on the botanical features of arid regions.

¹ Plant habits and habitats in the arid portions of South Australia. W. A. Cannon. Carnegie Inst. Wash. Pub. No. 308, 1921, p. 131.

² Biological relations of certain cacti. W. A. Cannon, American Naturalist, vol. 40, p. 27, 1906.

It was originally planned by the writer to include in the series as many studies on distinctive deserts as might be practicable, to be concluded by a physiological-ecological work of a comprehensive nature on deserts in general. In a research of this scope and nature the results of laboratory experimentation, by myself and others, are carried into the field to explain so far as possible the great variety of features associated with living plants there observed. While thus it is possible, as well as desirable, for different persons to provide the experimental background, it is clearly advantageous, if not indispensable, that one and the same person make the studies in the field. A comparative view, necessary to work of this scope, is thus obtained, and there are other advantages which need not be dwelt on in this place.

To attempt to apply to foreign and unvisited arid regions conclusions narrowly won is at once dangerous and may be highly misleading. Each separate arid region has problems of its own which require specific study. Even the common fact of aridity is exceedingly complex, possibly with unlike causes and characteristics as well as with dissimilar physiological and ecological relations.

Referring now to the general course of the studies on the plants, and their environment, of southern Africa as developed in this paper, the following main subjects are considered: (1) the perennial flora of the more arid regions; (2) the climatic environment; (3) plant habits and plant habitats; (4) comparative structure of leaves; and (5) the transpiring power of leaves.

The fact that Europeans have visited and lived in southern Africa since the last part of the fifteenth century, and that not only has much attention been given to the interesting flora, but that weather records have been kept continuously more than 100 years, are of decided assistance to persons interested in the African plants and in their physical environment. Thus, the course of the temperature and that of the rainfall, at least for certain stations, are well known; but as to other climatic features, particularly evaporation, the data are not so complete. It was in part to contribute to the general knowledge of evaporation in the arid portions of southern Africa, but more by way of better defining special habitats, that the writer carried atmometers and put them into operation there. Through the cooperation of several persons, the instruments were set up and read at different stations, including the ones visited by the writer, and certain comparative results were obtained. The work thus begun was taken over by the Botanical Survey of the Union and is now going forward under its auspices.

In the transpiration studies, the Stahl-Livingston cobalt-chloride method was employed, and the form of apparatus actually used was

especially planned and developed by Livingston for the South African work. As constructed, the apparatus was found to be easily carried about, and to be safely taken on treks in Cape carts, for example, where more fragile and larger apparatus might easily be damaged. The importance of obtaining comparative transpiration values, in work of this kind, is unquestioned. Thus, the transpiring power of the leaves of several representative species was observed, some of which are infrequently seen by botanists. Of these *Welwitschia mirabilis* of the Namib Desert was one. The demonstration of a relatively high index of transpiring power of its leaves was a matter of interest and appears to denote the essentially schlerophyllous nature of the rare species.

The habit-habitat studies were conducted on several lines. The local distribution was observed as accurately as possible, and in this quadrats were employed and the camera freely used. The latter also provided the means of preserving plant habits, whether of shoot or of root. As to special root studies, however, it should be stated that the writer was regrettably obliged to restrict his observations to a relatively few species. At the same time, it was keenly realized that possibly no region exists which would better repay intensive studies on roots in the field than the arid portions of southern Africa.

The perennial species of arid southern Africa are more or less closely related to species now occurring in humid districts not far distant. The matter of the direction of descent need not be considered here. In certain families the direction is apparently toward the more xerophytic, but in others it is in the opposite direction. However this may be, a study of structure indicates what tissues may have been directly affected by the arid habitat, in what way, and to what extent. Thus in some instances it may be possible to connect the course of morphological development with physiological processes as being causative, although in other instances such relation may not be clear. New structures have doubtfully arisen, as mentioned above, but, on the other hand, family characteristics can often be identified and have apparently survived when not inimical to the survival of the species.

In a study like the present one, of rather limited scope and greatly restricted as to time, it is impossible to go far without the cooperation of botanists, other scientists, and non-scientific but interested persons. Such cooperation, at once spontaneous and most generous, was not in the least wanting in the present instance. Although it is impossible to acknowledge specifically all of the favors and aid received, special acknowledgment should be made to the following: In connection with the atmometric work mainly, Professor R. H. Compton, University of Cape Town and the National Botanic Gardens, Kirstenbosch; Dr. Halm, Royal Observatory, Cape Town; Professor S. Schonland,

Albany Museum, Grahamstown; Professor J. W. Bews and Mr. R. D. Aitken, Natal University College, Pietermaritzburg; Mr. J. Patterson, Matjesfontein; Mr. R. Watson, Beaufort West; Dr. E. Reuning and Mr. Buvholz, Swakopmund; Miss Santa J. Smuts, Irene and Pretoria; Dr. E. P. Phillips, Division of Botany, Pretoria; and Mrs. A. B. Emery, Messina. It is a pleasure to acknowledge the interest of P. S. M. Arbuthnot, esq., Wynberg, as whose motor guest the writer enjoyed a special trip along the south coast to Mossel Bay and George, and to Oudtshoorn, in the Little Karroo. Miss Michell, Miss Stevens, and Professor D. Thoday, University of Cape Town, were helpful in many ways, especially in assisting the writer to become better acquainted with the vegetation of Namaqualand through the labors of the late Professor Pearson, some of the fruits of which are deposited at the university. Col. Dr. and Mrs. Buist, Matjesfontein, placed their excellent Karroo garden at the disposal of the writer and were helpful in many other ways. Through Mr. C. Steward, Chief Meteorologist, Department of Irrigation, data on the rainfall of the Union were obtained. Mrs. L. Bolus, Bolus Herbarium, Cape Town, determined a portion of the plants which were studied in the field, and the balance were determined by Dr. R. Marloth, Cape Town. Two special acknowledgments must be made: Dr. Marloth, who has especial knowledge of the plants of the Karroos, generously advised and assisted in very many ways. Botanical excursions to Table Mountain and to the Central Karroo were made under his guidance. And, finally, Dr. I. B. Pole Evans, Chief, Department of Botany and Director of the Botanical Survey, supported the work in a wholehearted fashion, and lent his aid in too many ways to give in detail. An eventful and most useful and interesting motor trip was enjoyed in his company to the Low Veld, Messina, and it was largely because of the interest of Dr. Pole Evans that the writer enjoyed the courtesy of transportation on the railways of the Union, without which his travels would necessarily have been much less and his results correspondingly cut down. Dr. Pole Evans also actively supported the atmometry begun by the writer and which was later taken over by the Botanical Survey.

The itinerary included, in addition to the motor trips as above mentioned, journey by railway across the Central or Great Karroo to De Aar, thence through the Protectorate of Southwest Africa to Swakopmund, returning to Cape Town. Later Pretoria was visited, and in late spring Pietermaritzberg and Durban. The months of August, September, and October were spent at Beaufort West and Matjesfontein, and at certain stations between, when more intensive studies on the plants, with especial regard to their transpiring power, were carried on. The seasons of the visit, therefore, included winter and spring.

LIST OF SPECIES AND GENERA.

- Acanthosicyos horrida* Welw.
Adansonia digitata L.
Adenia schlechteri Harm.
Aloe schlechteri Schönl.
 striata Haw.
 variegata L.
Anacampseros papyracea E. Mey.
Antizoma capensis Thunb.
Aptosimum indivisum Burck.
Arthræua leubnitzii Schinz.
Asclepias filiformis (?).
Asparagus capensis L.
 stipulaceus Lam.
 striatus Thunb.
Aster filifolius Vent.
Bauhinia marlothii Engler.
Berkheya obovata (Thunb.) Willd.
Bulbine rostrata (Jacq.) Willd.
Cadaba juncea (L.) Benth.-Hook.
Carissa ferox (?).
Celosia spathulifolia Engler.
Chænostoma sp.
Chrysocoma tenuifolia Berg.
Cotyledon coruscans Haw.
 decussata Sims.
 hemisphærica L.
 mamillaris L.
 orbiculata L.
 paniculata L. f.
 reticulata Th.
Crassula columnaris L.
 lycopodioides L.
 perfossa Lam.
 pyramidalis L.
 quadrangularis Schönl.
 tetragona L.
Cussonia spicata Thunb.
Dicoma diacanthoides Less.
Elytropappus rhinocerotis (L. f.) Less.
Eriocephalus glaber Thunb.
Euclea undulata Thunb.
Euryops lateriflorus Less.
 tenuissimus Less.
Euphorbia cooperi N. E. Br.
 eustacei N. E. Br.
 mauritanica L.
 multiceps Berger.
 mundii N. E. Brown.
 stellæspina Haw.
 stolonifera Marl.
Galenia africana L.
Garuleum bipinnatum Less.
Gazania pinnata (Thunb.) Less.
Geigeria passerinoides (L'Her.) Harv.
Gnaphalium sp. (?).
Grewia cana Sond.
Gymnosporia buxifolia (L.) Szysz.
Helichrysum ericifolium Less.
Hermannia candicans Ait.
Hyobanche glabrata (?).
Indigofera sp. (?).
Kleinia articulata Haw.
 radicans DC.
- Lebeckia psiloloba* Walp.
Loranthus glaucus Thunb.
Lycium spp. (?).
Mesembryanthemum anatomicum Haw.
 angulatum Thunb.
 bolusii Hook. f.
 brevifolium Ait.
 calamiforme L.
 croceum Jacq.
 crystallinum L.
 densum Haw.
 floribundum Haw.
 haworthii Don.
 junceum Haw.
 magnipunctatum
 Haw.
 nobile Haw.
 pygmæum Haw.
 quadrifidum Haw.
 spinosum L.
 splendens L.
 uncinatum Mill.
 uniflorum (n. s., Mrs.
 Bolus, not pub.).
 viride Haw.
 (n. s. ?).
Monechma sp. (?).
Nemesia sp. (?).
Osteospermum sp. (?).
Othonna pavonia E. Mey.
Pachypodium bispinosum (L. f.) DC.
Pelargonium alternans Wendl.
 crithmifolium Sm.
Peliostomum sp. (?).
Pentzia virgata Less.
Pteronia flexicaulis L. f.
 glomerata L. f.
 incana Less.
 pallens L. f.
Protea neriifolia R. Br.
Relhania squarrosa (L.) L'Her.
Rhus lancea L.
 viminalis Vahl.
Rhus sp. (?).
Royena pallens Thunb.
Salsola aphylla L. f.
Selago sp. (?).
Senecio cotyledonis DC.
 longifolius L.
Sesamnothamnus lugardii (?).
Stachys sp. (?).
Stapelia pillansii N. E. Br.
Stoebe sp. (?).
Sutherlandia frutescens R. Br.
Tetragonia sp. (?).
Thesium horridum Pilger.
 spinosum F. f.
Tripteris sinuata DC.
Ursinia sp. (?).
Viscum rotundifolium L. f.
Welwitschia mirabilis Hook.
Zygophyllum stapfii Schinz.

GENERAL FEATURES OF THE CLIMATE OF
SOUTHERN AFRICA.

The leading features of the climatic environment of plants of arid regions can be said to lie in the temperature and its variation, in the intensity of light, and in the amount and seasonal distribution of the rainfall, together with certain other related factors, including the frequently low relative humidity. A change in one of these, particularly in the amount or the season of the rains, very profoundly modifies the rest, with consequent serious alteration in the environic complex as a whole. Thus, when the rainfall is in the cool season only, when the temperature is low, the humidity high, and the light values low, the aridity of the drought period is accentuated by the fact of high temperatures, low relative humidity, and high light values. When, on the other hand, the rainy period coincides with the warm season, the period of drought is not so markedly arid, for the reason that the temperature at the time is relatively low, with correspondingly high relative humidity and relatively low light intensity. Accordingly, it is not difficult to understand why, in regions of winter rainfall, the perennials should have pronounced xerophytic characteristics, even if the amount of rain be considerable. In regions with equal precipitation, but occurring the one in the cool and the other in the warm season, it appears to be the rule that the former is the more arid. In certain arid and semi-arid regions of the world both types of rainfall occur. In such event, if the rains of summer and of winter are fairly large, as in southern Arizona, the vegetation is correspondingly abundant, but in case the periodic rains are uncertain, both as to amount and season, the arid conditions may be intense. The latter obtains in central Australia and in a portion of South Africa, especially in the Karroos. A zone, in which lie the Karroos, extending north-westerly from Algoa Bay, separates the region to the west with rains in winter from the balance of the country with summer rains. In this intermediate belt the precipitation may tend toward the one or the other type, and vary from season to season in this regard. It also may be of small amount or may wholly fail. It is this zone, including Namaqualand to the west, which constitutes the most arid portion of the subcontinent.

Southern Africa has a mild temperate climate. In the interior the summers are hot and the winters are cool, with heavy frosts and snow in the mountains.

The rainfall is mainly periodic. A line extending northwest from Algoa Bay separates the regions on the east, with rains mainly in summer, from those on the west, mainly with winter rains (fig. 6, p. 22). In the west-central and extreme western portions the rainfall may be small in amount. Here are the Karroos, the Kalahari, and Nama-

qualand. But in the extreme southwest, and in the south, east, and east-central portions of the subcontinent the rainfall is plentiful and the vegetation is varied and may be abundant.

The physical factors which appear to mainly control the climate are latitude, topography, proximity to the oceans, and relation to regions of permanent low atmospheric pressure both to the east and to the west.

The main facts in regard to the physiographical characteristics are succinctly stated by Cox,¹ as follows:

"There are essentially four elevated plateaux; the Coast Flats, with an elevation of 500 to 600 ft., and a variation in width from thirty miles in Southwest Africa to three miles or even less in the southeast of the Cape Province; the Little Karroo, a narrow stretch of from fifteen to twenty miles, with an elevation of about 1,500 ft.; the Great Karroo at an altitude of from 2,000 to 3,000 ft., and the Northern Karroo with an elevation of 4,000 ft., rising to 6,000 ft. in the eastern portions. These plateaux are separated by steep escarpments, rising a considerable height above them." (Fig. 1.)

Variations in physiography affect the climate mainly along two lines. On the one hand, differences in altitude tend to overcome differences in latitude, and on the other they directly affect rainfall. Referring to the former, Cox presents data in which it appears that although the difference in latitude between Pretoria and Mossel Bay, for example, is nearly 9°, the mean annual temperature is almost the same. Pretoria is approximately 4,000 feet greater in altitude than Mossel Bay. So far as the effect of mountains on rainfall is concerned, it will suffice to remark here that aside from the increase with altitude, as in mountains, mountains also serve to remove moisture from the passing air-currents, so that they may not deposit moisture on adjacent lower lands. Such is the condition in the Karroos, which are separated from each other and from the coast by mountain chains where the rainfall decreases in general from the coast inland, as from the southern to the northern Karroos.

The relatively small land area with long shore-line and with immense bodies of water on three sides, are important factors in the shaping of the southern African climate. On the west is the cold Benguela current of the southern Atlantic, and on the south and east is the warm Mozambique current. The difference in temperature at the same latitude between the east and the west coasts is striking. Thus² at latitude 30°, which is about that of Durban, the mean monthly temperatures of the surface water somewhat off-shore for the months given are as shown at top of next page.

¹ A guide to botanical survey work. Botanical Survey of South Africa, Mem. No. 4, p. 27, 1922.

² Publication of the British Meteorological Office, Official No. 59.

	Feb.	May.	Aug.	Nov.
	° F.	° F.	° F.	° F.
Atlantic Ocean.....	66	65	60	62
Indian Ocean.....	75	74	69	72

Such differences in the temperature of the sea directly affect the temperature of coastwise stations. Thus, Port Nolloth, on the Atlantic, lat. $29^{\circ} 16'$, has a mean annual temperature of 57.5° F., and Port St. Johns, Indian Ocean, lat. $31^{\circ} 38'$, has a mean annual temperature of 66.9° F. (Cox, *l. c.*).

Not only do the ocean currents thus directly affect the temperature of adjacent points on shore, but in that they vary in capacity of delivering moisture to the air they are important in modifying the rainfall conditions as well; and in connection with the prevailing winds and other factors they may ultimately influence the rainfall in places as remote as, for example, the highlands of the Protectorate of Southwest Africa, 800 miles or more from the Indian Ocean.

The part played by high-pressure areas off the east and west coasts is outlined by Cox (*l. c.*) as follows:

“The seasonal distribution of rain is related to the movement and action of the permanent anti-cyclones which lie off the west coast of the Cape Province and off the east coast between the Cape Province and Australia. This belt of high pressure migrates northwards and southwards with the sun, and in addition the centres or cores have a lateral displacement from month to month. During April and May that to the east of the Cape Province moves westward to the African coasts, while that on the west coast moves eastwards. At the same time an important secondary core appears over the land, where barometric pressure increases until June or July. The movement northwards of the anti-cyclonic belt brings the west and southwest coastal regions of the Cape Province under the influence of A-shaped depressions connected with the cyclonic system to the south; and it is the westerly winds associated with the rear of these depressions which are the rain-bearers for the west and southwest coastal districts of the Cape Province, where over 75 per cent of the annual precipitation occurs during the winter. As will be seen, the area thus watered is not extensive. Originating in the cold parts of the Atlantic the capacity of the westerly winds for moisture is small, and after condensation, forced by the elevated ground which forms the western boundaries of the plateaux, they soon cease to act as rain-bearers.

“In September and October the high pressure moves off the land, merging into the South Indian anti-cyclone, which then returns eastwards to its summer position just off the west coast of Australia, and the South Atlantic anti-cyclone which lies a short distance from the west coast of the Cape Province. The north-easterly and easterly winds associated with the former introduce the moisture which is deposited over the greater part of the Union during the summer months. These winds when leaving the Indian Ocean are warm and their capacity for moisture is great; and although they deposit a considerable amount of moisture in ascending the plateaux . . . , and so decrease their absolute humidity, they still reach the interior with a comparatively high humidity.”

would be expected, all of which are especially well marked in the more arid regions. The mean extremes of the Cape Peninsula are 80° and 47° F. The mean for the warm season at the Cape is 69.7° and for the cold season is 58.4° F. For the southern Karroo the means of the two seasons are 75.5° and 51° F. For the central and western portions of the Central Karroo, in which are included Beaufort West and Prince Albert Road, as well as Matjesfontein and Laingsburg, the means are 58° to 59.6° F. for the warm season and 50° F. for the cold season. In the east Central Karroo the mean for the warm season is 78.7° F. In this division is included Aberdeen and Graaf Reinet. In the northern, or Upper Karroo, which extends from

TABLE 1.—*Temperature, in degrees Fahrenheit.*^a

	Mean tem- perature.	Mean.		Absolute.		Mean of absolute yearly.		Mean daily range.
		Max.	Min.	Max.	Min.	Max.	Min.	
Table Bay.....	61.3	80.0	47.0	101.3	34.1	101.3	34.1	10.6
Pietermaritzburg.....	66.3	79.7	52.9	109.0	27.0	106.0	32.0	26.8
Bloemfontein.....	61.9	75.4	48.4	101.7	22.0			26.5
Johannesburg.....	61.2	74.4	47.9	96.0	21.0			26.5
Graaf Reinet.....	64.2	78.7	49.6	108.0	29.7			29.1
Kimberley.....	65.8	81.5	50.2	104.3	21.5			31.3
Windhoek.....	66.5	79.2	53.9	98.3	26.5			25.3
Swakopmund.....	59.5	68.1	53.7	105.1	36.5			14.4
Walfisch Bay.....	59.5	65.9	53.2	94.8	34.9			12.7

^a Compiled from The climate of the continent of Africa. Alexander Knox. Cambridge, 1911.

a little to the east of Clanwilliam eastward, the mean temperature of the warm season is 70.7° to 72.3° F. and that of the cold season is 42.3° to 50° F. The means of the northern border, including the eastern parts of Namaqualand and Clanwilliam divisions, in which is Upington, are 78.5° and 51° F. As to absolute maximum temperatures, there have been recorded in the Cape Peninsula 101.3°; the Southern Karroo, 112°; West Central Karroo, 116.06°;¹ East Central Karroo, 108°; Northern Karroo, 110°, and the northern border, 112° F.

In Southwest Africa, according to Knox, the summers are hot, which applies to stations not on the seaboard, and the winters moderate, with not infrequent frosts in the interior. There is relatively wide range in daily and annual temperatures. At Windhoek, altitude 5,428 feet, the mean temperature of the warm season is 73.6° and of the cold season is 57.3° F. The mean annual temperature is 66.2°. The absolute maximum at Windhoek is 98.8° and the absolute minimum is 26.5° F. One of the characteristic climatic features of Windhoek is that the mean temperature, the mean maximum, and mean mini-

¹ Prince Albert, 1883. Das Klima des aussertropischen Südafrika. Dove, p. 66, 1888.

mum temperature, are very regular for the various months from year to year. Thus in course of four consecutive years, in March, the mean minimum temperature ranged between 57.7° and 58.6° F., and the mean maximum temperature for the same years ranged between 72.9° and 74.3° F. At Swakopmund the mean annual temperature is 59.5° ; in the warm season the mean temperature is 62.7° , and in the cold season it is 56.6° . The absolute maximum at Swakopmund is 105.1° and the absolute minimum is 36.5° F. At Swakopmund the presence of the ocean and of the summer fog are important controls of the temperature.

RAINFALL IN SOUTHERN AFRICA.

GENERAL CONDITIONS.

Where local circumstances do not intervene to prevent, the rainfall increases from the west to the east, and in a less marked manner and less constant, according to Knox, from the south to the north. Knox illustrates these conditions by citing the precipitation at Keetmanshoop, Southwest Africa, Vryburg, Bechuanaland, and Lourenco Marques, Portuguese East Africa, where the mean annual rainfall is 6.38, 22.38, and 28.23 inches, respectively, and also at a series of stations situated somewhat farther to the north. So far as the increase of the rainfall from the south to the north is concerned, Knox refers to Graaf Reinet, Central Karroo, mean annual rainfall 15.29 inches, Kimberley, in the northern border, 18.17 inches, and Vryburg, 22.38 inches. The altitude of Graaf Reinet is 2,463 feet, that of Vryburg 3,890 feet, and that of Kimberley 4,012 feet. The relief of South Africa is important in modifying the general rainfall. Thus, the rainfall of the table-land of Southwest Africa, in the neighborhood of Windhoek, is heavier than that of the Kalahari, with lower altitude, to the east, and the rainfall of the extreme southwest is relatively heavy, being, according to Knox, greater than in any other of the Cape districts. As before remarked, regions of high altitude have relatively heavy precipitation, which is of some importance in operating to modify, in certain particulars, features of the climate in the rain shadow of such highlands, or at any rate in contiguous regions of lower altitude. Under proper conditions of air-currents the relative humidity, and hence the evaporation, of such contiguous regions is probably directly and markedly affected by the regions of high rainfall. Although not sufficient study has been given this phase of the general subject (which is discussed elsewhere) to give satisfactory details, observations, nevertheless, appear to verify the statement. Another climatic factor, which such contiguity of regions would influence, is temperature, which need not be referred to further.

The general terrace formation of southern Africa, the fact of important mountain masses and chains which separate regions of unlike altitude, and which in a general way run parallel to the coast, are of moment in providing local conditions which serve to modify those generally obtaining. In the eastern portion of southern Africa, the coastal plateau is relatively narrow, but in the southern and south-western portions it is fairly wide, and several ranges of mountains intervene between the coast and the height of land relatively far inland. Thus, going northward from Knysna, one ascends and passes through the Outeniqua Mountains to the Southern Karroo, one crosses the Southern Karroo, ascends and passes through the Groote Zwatze Bergen, to the Central Karroo; and one crosses the Central Karroo to and through the Nieuweveld range to the Northern Karroo. The Southern or Little Karroo is between 1,000 and 2,000 feet, the Central Karroo between 2,000 and 3,000 feet, and the Northern Karroo 4,000 feet or more in altitude. The mountain ranges which separate the terraces have an altitude of from 3,000 to 6,000 feet. A very large proportion of southern Africa has an altitude of 4,000 feet, or more. It can be seen that the peculiar relief of southern Africa must be, as it in fact is, of importance in shaping the climate of this portion of the continent. It operates not only to modify the temperature, but the

FIG. 2.—Average annual rainfall. In part from Mem. 4, Bot. Sur. So. Africa, 1922.

rainfall as well. The higher altitudes serve to condense the moisture of moisture-laden winds coming from the east coast and from the west coast, and the precipitation in such areas may be large. But, on the other hand, more lowly lying but contiguous regions, in the lee of the highlands, may for this or other reasons have a small, or relatively small, annual precipitation.

The wettest station so far reported in South Africa is Maclear's Beacon, Table Mountain, where the average for seven years, 1894 to 1900, was 86.8 inches annually.¹

TABLE 2.—Seasonal distribution of rainfall.^a

	No. of years.	Average annual rainfall, in inches.	Percentage of seasonal rainfall, with amount, in inches, in parenthesis.			
			Dec.—Feb.	Mar.—May.	June—Aug.	Sept.—Nov.
Cape Town.....	59	25.09	7 (1.7)	26 (6.1)	48 (10.1)	19 (4.5)
Grahamstown.....	43	26.36	26 (7.9)	26 (7.9)	11 (3.3)	37 (10.9)
Pietermaritzburg ...	26	37.13	42 (14.4)	21 (7.5)	5 (1.8)	31 (10.7)
Ladysmith.....	39	14.08	22 (3.2)	30 (4.4)	25 (3.6)	23 (3.3)
Montagu.....	39	12.8	13 (1.6)	30 (3.8)	34 (4.4)	23 (3.0)
Oudtshoorn.....	42	9.45	20 (1.7)	29 (2.4)	19 (1.6)	32 (2.7)
Uniondale.....	42	13.42	19 (2.6)	29 (0.4)	25 (3.3)	26 (3.5)
Aberdeen.....	39	12.19	37 (4.4)	30 (3.6)	9 (1.0)	24 (2.8)
Beaufort West.....	43	9.56	32 (2.9)	36 (3.4)	10 (0.9)	22 (0.2)
Graaf Reinet.....	40	13.87	30 (4.5)	31 (4.7)	9 (1.3)	30 (4.5)
Laingsburg.....	18	4.47	20 (0.8)	36 (0.6)	27 (1.2)	17 (0.7)
Matjesfontein.....	33	6.5	17 (1.1)	33 (2.1)	24 (1.6)	24 (1.5)
O'okiep.....	26	6.73	9 (0.6)	31 (2.0)	41 (2.6)	19 (1.2)
Upington.....	28	10.81	38 (4.1)	33 (3.57)	2 (0.19)	17 (1.9)
Pretoria.....	18	26.9	55 (14.8)	17 (4.58)	2 (0.45)	27 (7.1)
Pietersburg.....	17	20.6	58 (12.0)	17 (3.5)	2 (0.5)	22 (4.6)
Messina.....	11	14.2	69 (9.8)	12 (1.7)	1 (0.2)	18 (2.5)
Warmbad.....	6	5.6	36 (2.0)	45 (2.5)	8 (0.5)	11 (0.6)
Luederitz Bay.....	6	2.8	32 (0.9)	17 (0.5)	43 (1.2)	7 (0.2)
Keetmanshoop.....	6	6.3	47 (3.0)	35 (2.2)	2 (0.1)	16 (0.1)
Bethany.....	6	5.3	51 (2.7)	34 (1.8)	2 (0.1)	13 (0.7)
Gibeon.....	6	7.5	55 (4.1)	34 (2.6)	1 (0.1)	9 (0.7)
Swakopmund.....	6	0.98	71 (0.7)	18 (0.18)	0	10 (0.1)
Windhoek.....	14	15.08	54 (8.2)	37 (5.2)	2 (0.26)	9 (1.3)
Gobabis.....	6	15.4	59 (9.2)	29 (4.5)	0	11 (1.7)
Karibib.....	6	7.7	65 (5.0)	35 (2.7)	0	0
Grootfontein.....	6	23.13	60 (13.8)	28 (6.7)	0	11 (2.5)

^a The data are mainly from the Meteorological Office, Pretoria, and from Knox, The climate of the continent of Africa, Cambridge, 1911. Where there are differences between the "average" rainfall and the sum of the seasonal rains, the reason lies in the differences in the data on which they are based.

It will be of interest now to review in some detail some of the leading characteristics of the rainfall of representative stations of the Union and of the Protectorate of Southwest Africa. Although in doing so attention will be especially directed to regions of which the study principally deals, that is, those having a small rainfall, it will nevertheless be instructive to refer to the rainfall conditions of certain other

¹ Science in South Africa; The meteorology of South Africa. C. M. Stewart. Page 28, 1905.

regions, not necessarily very remote, in which the rainfall is relatively or actually large, and which for this reason have a marked influence on the climate of the regions first referred to above, that is, those in which the annual precipitation is relatively or actually small.

It has already appeared, and is generally known, that a marked feature of the rainfall of South Africa taken as a whole is its periodicity. There are regions, however, in which the periodicity of the rainfall is not an especially prominent feature, but between the Cape and Natal, not to mention other sections of the Union, there is a region in which the rainfall is fairly well distributed through the four seasons. Knysna, George, and Grahamstown are located in this intermediate region. The annual precipitation, especially of the two first given, is uniformly distributed, and also that of Grahamstown, but not, however, so uniformly. The statistics of rainfall for Grahamstown are at hand, and will be referred to as representing the region. The precipitation at Grahamstown averages 26.36 inches, of which about 25 per cent occurs in summer, 26 per cent in autumn, 36 per cent in spring, and somewhat more than 11 per cent in winter. The relative dependability of the rainfall at Grahamstown can be further seen from the accompanying table on rainfall extremes. Here it will be noted that the

FIG. 3.—Seasonal distribution, in percentages, of rainfall. Adapted from Mem. 4, Bot. Sur. So. Africa, 1922.

yearly extremes at Grahamstown are 42.52 and 17.78 inches, that the extremes for summer, autumn, and spring are relatively small, and that the actual rainfall for the three seasons is relatively large in amount. But, on the other hand, during the winter the rainfall is not only small, but also it is relatively variable. The dependability of the rainfall at Grahamstown can be illustrated in yet another way. Referring to table 3, which gives the periods having less than 0.15 inch rainfall per month, it will be seen that at Grahamstown about three months every year have rain of this small amount, and that the rainfall of spring and of summer is always more than 0.15 inch per month, but that of the total yearly precipitation occurring in this small monthly amount 90 per cent is in winter. It thus appears that at Grahamstown, and probably also in this general region, the rainfall is periodic, but not particularly small, and it does not wholly fail in any season. These features, as is pointed out in another place, are of undoubted importance in modifying to a certain limited extent the severe conditions of aridity in certain arid regions, especially the Karroos, further to the north.

When one goes much to the west, or to the east of the intermediate region just spoken of, the rain may be found to increase, or may not, but in any event, the periodicity of the rainfall becomes an increasingly

FIG. 4.—Rainfall for January 1920. Adapted from weather report.

prominent characteristic of the climate. At Cape Town the average rainfall is 25.09 inches, of which 0.17 per cent occurs in summer, 25 per cent in autumn, 47 per cent in winter, and 19 per cent in spring; or, in other words, approximately four-fifths of the total average rainfall at Cape Town occurs in six months, March to August, leaving the balance of the year with little rain. At Pietermaritzburg, on the other hand, with a rainfall of 37.13 inches, about 41 per cent occurs in summer, 21 per cent in autumn, 31 per cent in spring, and only 5.8 per cent in winter. These two stations also can be used to illustrate other conditions attending the rain of winter and drought of summer on the one hand, and the rain of summer and drought of winter on the other. Thus, the rainfall extremes at both Cape Town and Pietermaritzburg are a characteristic of the climate of each. At Cape Town the yearly extremes are 33.98 and 17.52 inches, and at

TABLE 3.—*Drought periods (periods with less than 0.15 inch rainfall in a month, or no precipitation).*^a

	Length of record in years.	Average yearly drought period in months.	Seasonal percentage of drought period.			
			Dec.—Feb.	Mar.—May.	June—Aug.	Sep.—Nov.
Cape Town.....	59	0.93	83.6	12.7	0	3.6
Grahamstown....	43	0.23	0	10.0	90.0	0
Pietermaritzburg.	26	1.6	0	11.9	88.09	0
Ladysmith.....	39	1.2	44.6	17.0	10.6	27.6
Montagu.....	37	2.2	57.3	18.2	6.0	18.2
Oudtshoorn.....	42	2.2	43.1	18.9	15.7	22.1
Uniondale.....	42	1.2	53.8	17.3	19.2	9.6
Aberdeen.....	39	3.0	12.0	14.9	51.4	21.49
Beaufort West...	43	3.1	19.8	13.9	40.0	25.7
Graaf Reinet....	40	2.1	16.4	8.3	51.7	22.1
Laingsburg.....	18	5.2	34.0	17.0	17.0	31.9
Matjesfontein....	33	3.9	35.3	20.0	15.3	29.2
O'okiep.....	26	5.9	42.5	17.4	9.6	30.0
Upington.....	28	5.2	16.8	14.2	44.1	24.6
Pretoria.....	18	3.2	0	17.2	70.0	12.0
Pietersburg.....	17	3.8	1.5	20.0	63.9	15.3
Messina.....	11	5.1	0	22.7	49.1	28.0
Warmbad.....	^b 6	5.9	10.0	23.3	30.0	36.6
Luederitz Bay....	^b 6	7.7	15.7	28.9	21.0	34.2
Keetmasnhoop...	^b 6	5.5	3.1	18.6	46.8	31.2
Bethany.....	^b 6	6.5	3.0	21.2	45.4	30.3
Gibeon.....	^b 6	6.2	8.1	2.7	48.6	32.4
Swakopmund....	^b 6	9.5	14.8	27.6	31.8	25.5
Windhoek.....	6	5.3	0	15.6	53.1	31.2
Gobabis.....	6	4.8	0	20.6	58.6	20.6
Karibib.....	^b 6	5.9	0	20.5	52.1	26.5
Grootfontein.....	6	4.8	0	20.0	60.0	20.0

^a Compiled from meteorological records; those for the Union of South Africa furnished by the Meteorological Office, Pretoria, and those for Southwest Africa taken from Arbeiten d. Farmwirtschaft-Gesellsch. f. Südwest Afrika, Bd. 2. May, 1921.

^b Records not complete; those for Warmbad, 58 months; for Luederitz Bay, 61 months; for Keetmanshoop, 65 months; for Gibeon, 71 months; for Swakopmund, 58 months; and for Karibib, 71 months.

FIG. 5.—Rainfall for August 1920. Adapted from weather report.

FIG. 6.—Minimal rainfall, 1885-1894. In part after Marloth, Das Kapland. The heavy line running northwest from near Port Elizabeth approximately separates the region of summer rains, to the east, from that of winter rains.

Pietermaritzburg they are 54.43 and 25.19 inches. As table 4 shows, the seasonal and the monthly extremes are at each station a marked characteristic of the rainfall. When we compare the relative amount of rain that occurs in monthly amounts less than 0.15 inch, we find, however, that the average yearly total of such small amount is somewhat less at Cape Town than at the station in Natal, indicating that there are fewer days with a small rainfall at Cape Town than at

TABLE 4.—*Rainfall, in inches, compiled from meteorological records.*^a

	Yearly extremes.		Seasonal extremes.								Monthly extremes.		Daily max.
			Dec.-Feb.		Mar.-May		June-Aug.		Sept.-Nov.				
	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	
Cape Town.....	33.98	17.52	5.50	0	12.45	1.45	22.30	4.38	7.96	2.65	13.27	0	3.88
Grahamstown.....	42.52	17.78	2.87	2.16	3.12	2.08	1.62	0.67	4.55	3.10	10.69	0	7.28
Pietermaritzburg....	54.43	25.19	30.98	9.22	13.43	3.18	7.72	0	25.80	4.67	13.36	0	5.85
Ladysmith.....	21.79	7.67	5.74	0.29	8.97	0.77	7.20	0.84	6.75	0.55	6.36	0	4.06
Montagu.....	22.08	7.66	7.37	0	8.70	1.19	7.6	0.98	5.90	0.69	7.59	0	6.75
Oudtshoorn.....	21.46	7.12	4.00	0	7.39	0.64	4.7	0.39	9.83	0.67	3.9	0	3.75
Uniondale.....	28.11	7.33	5.35	0.31	12.88	0.95	8.5	1.18	10.75	0.67	10.48	0	7.67
Aberdeen.....	19.23	4.18	9.70	1.00	8.30	0.84	4.18	0.03	7.50	0.26	5.72	0	3.92
Beaufort West.....	18.26	3.19	9.12	0.43	9.85	0.85	2.5	0.10	5.70	0.23	9.70	0	8.08
Graaf Reinet.....	21.46	5.79	10.2	1.32	9.73	1.17	4.73	0.04	7.66	0.39	5.26	0	6.50
Laingsburg.....	7.10	1.06	2.82	0	4.36	.29	2.19	0	2.00	0	3.18	0	1.75
Matjesfontein.....	10.38	2.16	4.90	0	6.13	0	5.17	0	4.73	0	3.30	0	2.06
O'okiep.....	11.7	3.46	2.55	0	6.04	0.63	6.17	0.70	3.34	0.11	3.49	0	2.04
Upington.....	15.52	1.33	6.99	0.09	9.8	0.51	1.59	0	5.6	0	7.4	0	2.52
Pretoria.....	55.90	16.68	35.82	6.78	11.11	2.09	4.05	0	10.57	4.81	22.12	0	5.33
Pietersburg.....	31.53	10.47	20.77	5.51	6.77	0.56	2.71	0	8.73	1.47	12.18	0	4.30
Messina.....	22.05	9.40	7.63	2.71	4.29	0.29	1.20	0	6.03	0.39	8.63	0	5.28

^a Supplied by the Meteorological Office, Pretoria.

Pietermaritzburg. Such, as a matter of fact, is the case. From data furnished by the Meteorological Office, it appears that at Cape Town there are on an average 36.3 days of rain every year during which the rain amounts each day to 0.1 inch or less, while at Pietermaritzburg the number of days with such small rainfall each year averages 57. The Cape Town type of rainfall, with modifications, especially as to amount, holds in a general way in western South Africa, while the Pietermaritzburg type is characteristic, also with modifications, for central and eastern South Africa, and to a degree as far west as the highlands of Southwest Africa. In an intermediate zone, as above referred to and elsewhere mentioned in greater detail, neither the one or the other type prevails, but the influence of both is felt. And in the highlands, especially of the eastern portion of the Union, the rainfall is fairly uniformly distributed through the year.

RAINFALL IN THE LITTLE KARROO.

Turning now from the consideration of certain features of the rainfall at stations on or near the coast, we will examine some of the leading rainfall characteristics of stations in the interior, and first of all, of certain of those in the Little Karroo. Ladysmith, Montagu, Oudtshoorn, and Uniondale may be taken to represent the Little Karroo, so far as the rainfall of that region is concerned. These stations are situated in a fairly east-west line, the order from the west being Montagu, Ladysmith, Oudtshoorn, and Uniondale. As table 2 indicates, the rainfall at Montagu is 12.8 inches annually, at Ladysmith 14.08 inches, at Oudtshoorn 9.45 inches, and at Uniondale 13.42 inches. Situated as they are in the zone separating the two well-marked rainfall regions on the east and on the west, all of these stations show to a degree the influence of both types of rainfall. An examination of table 2 will show that the seasonal percentages of precipitation in the Little Karroo exhibit considerable uniformity, recalling in this respect the stations nearer the coast. At Montagu the heaviest rainfall is in winter and the least in summer, which is also true of all the other stations, except only Oudtshoorn, at which the winter rainfall is the least. The average length of the drought periods of winter at Montagu and Ladysmith is relatively less than at the other stations farther to the east, and indicates the influence of the western type of rainfall. As to the rainfall extremes, it is of interest to note, whatever may be the significance, that the yearly minima for both stations is about the same, between 7 and 8 inches, and the yearly maxima of Montagu, Ladysmith, and Oudtshoorn lie between 21 and 22.08 inches, while the maximum at Uniondale is about 28 inches. The seasonal extremes at Uniondale appear also, on the whole, to be the most marked, the maximum for autumn being 12.8 and the minimum 0.95, and the maximum and minimum of spring being 10.7 and 0.67 inches. Uniondale has also experienced the greatest monthly extremes of rainfall, and also one of the heaviest daily precipitations recorded in the Union, namely, 7.67 inches. The length of the average period each year having 0.15 inch per month rain, or no rainfall, for Montagu and Oudtshoorn is 2.2 months, and for Ladysmith and Uniondale 1.2 months. The total number of months with no recorded rainfall at Montagu for 37 years is 59; at Ladysmith, for 39 years, 17; at Oudtshoorn, for 42 years, 29; and at Uniondale, for 42 years, 16 months. The average for these stations is, respectively, 1.69, 0.43, 0.69, and 0.38 months each year without rain. When we subtract the length of the rainless period from the length of the period of drought, as here defined, to get the average length of periods having less than 0.15 inch rain each year, it appears that Montagu has the least, 0.51 month, and Oudtshoorn the greatest, 1.51 months. This accords well with the actual number of days each year in which the average rainfall is 0.10 inch, or less, and

suggests that the average rainfall, per storm, is larger at Montagu than at the station further east. The following are the average number of days during which in each year the rain amounts to less than 0.10 inch: Montagu, 5.9; Ladysmith, 19.4; Oudtshoorn, 13.6; Uniondale, 18.9. That the average storm may be somewhat larger at Montagu and smaller at Oudtshoorn also appears from the data given by Marloth,¹ from which it may be found that the average daily storm at the four stations in the order above given is as follows: 0.39, 0.29, 0.25, and 0.28 inch.

Without entering into a fuller discussion of the rainfall of the Little Karroo, it will be apparent that as a whole it is fairly uniform, or at least that it shows less marked periodicity than stations much to the west or to the east. This is due in part to the position of the area and also in part, according to Marloth,² to the influence of near mountains, as at Ladysmith. However, the station is clearly under the influence of the western type of rainfall, as would appear from the fact that over 34 per cent of the rainfall of the place occurs in winter.

RAINFALL OF THE GREAT OR CENTRAL KARROO.

The stations which have been selected to represent the rainfall conditions of the Great Karroo are Aberdeen and Graaf Reinet on the extreme east, Laingsburg and Matjesfontein on the extreme west, and Beaufort West, which is somewhat to the east of the central portion. From east to west, as mentioned in another place, the Great Karroo extends for a distance of between 200 and 300 miles, and it lies from 80 to 140 miles from the south coast, being nearer on the west. The situation of the stations is such, as will appear directly, that those to the east are under the influence of the eastern type of rainfall, and those to the west are more or less under the influence of the western type; that is to say, that at Aberdeen, Graaf Reinet, and Beaufort West a relatively large amount of rain falls during the warm seasons (spring, summer, and autumn), while at Laingsburg and Matjesfontein there is a relatively large percentage of rainfall during the winter season, although in the west the distribution of the rainfall throughout the year is much more uniform than at the stations further east.

ABERDEEN AND GRAAF REINET.

The average rainfall at Aberdeen is 12.19 and at Graaf Reinet it is 13.87 inches. At Aberdeen the average rainfall of summer is 36.7 per cent of the total, and at Graaf Reinet it is 29.6 per cent. The winter rains at the two stations are 8.9 and 8.6 per cent of the average, respectively. The rainfall of autumn at Aberdeen is 30.4 per cent

¹ A guide to botanical survey work. Bot. Survey So. Africa, Memoir No. 4. Issued by the advisory committee for the botanical survey of South Africa. Pp. 40-42. 1922.

² Das Kapland, etc. Wissensch. Ergebnisse deutsch. Tiefsee-Expedition, 2d Bd., 3 Th., p. 257. 1908.

and at Graaf Reinet 31.1 per cent, but the rain in spring at Aberdeen is 23.7 per cent, while at Graaf Reinet it is 29.7 per cent of the annual average rainfall. The differences in the distribution of the rain throughout the year at the two stations can presumably be accounted for by the relation to the mountains, which, in the case of Aberdeen, lie to the north, and in the case of Graaf Reinet lie to the east and to the west as well.

Turning now to the rainfall extremes, it is interesting to note that the maximal rainfall for the year, for the seasons, and for the month, at both stations, is about the same; the same is true also for the minimal rainfall, but Graaf Reinet has experienced the larger daily maximum. In one day 6.5 inches of rain was reported to have fallen at Graaf Reinet, while the largest reported rain occurring on one day at Aberdeen was 3.9 inches. There is a considerable apparent difference between the two stations as to the average length of the drought periods. At Aberdeen the average yearly dry period is 3 months; at Graaf Reinet it is 2.1 months. As for the seasonal differences in the length of the drought periods, it will be seen from table 3 that the percentage in winter, for the two stations, is almost the same, namely, 51.4 for Aberdeen and 51.7 for Graaf Reinet. In Spring, at Aberdeen, occurs 21.49 per cent of the drought of the year, and at Graaf Reinet, for the same season, the percentage is 22.1. In summer, however, the drought period is longer at Graaf Reinet than at Aberdeen, 12 at the former as opposed to 16.4 per cent at the latter station, but in autumn the ratio is in the opposite direction and is considerably greater. Thus, at Graaf Reinet the autumnal drought period is 8.3 per cent of the whole and that at Aberdeen is 14.9 per cent. These seasonal differences in the length of the drought period at Aberdeen and Graaf Reinet correspond very well with the differences in seasonal precipitation, as represented by percentages of the total rainfall at the stations, as is shown in table 2, and may have for their leading cause local features, such as variation in topography, or unlike relation to neighboring highlands, which, as was pointed out above, may be influential in molding certain characteristics of the rainfall, as at Ladysmith and other places.

At Aberdeen the average length of the dry spells during which no rainfall was reported, for a period of 39 years, is 1.4 and at Graaf Reinet it is 0.85 month. By subtracting these amounts from the drought periods as given in table 3, the periods during which the rainfall averaged less than 0.15 inch in each month can be arrived at. Thus, in the case of Aberdeen it is 1.6 and in that of Graaf Reinet it is 1.25 month, suggesting that at the former station there may be more rain of this character than at the latter.

The average number of rainy days at Aberdeen is 41 and at Graaf Reinet 52, making the average daily amount of rain during rainy

periods at the two places 0.29 and 0.25 inch, respectively, which is possibly to be attributed to the greater percentage at Aberdeen of summer precipitation. The frequency of long spells of continuous rain appears to be characteristic. Thus, at Aberdeen, during 39 years, nine such spells were recorded, with an aggregate of 17.83 inches. These long stormy spells were in summer, autumn, and spring. At Graaf Reinet, in 40 years, but three such stormy spells were recorded, with an aggregate rainfall of 5.05 inches, occurring in summer and in spring.

BEAUFORT WEST.

Beaufort West has an average annual rainfall of 9.56 inches, of which 31.8 per cent is in summer, 36.1 per cent in autumn, 10 per cent in winter, and 21.8 per cent in spring. The actual seasonal amounts are: 2.9, 3.4, 0.9, and 2 inches. The mean annual number of days on which rain occurs at Beaufort West, according to Marloth, cited above, is 36, which gives the average amount of rain for each rainy day as 0.36 inch. But the amount of rain falling in one day may be very considerable, as, for example, it was recorded that 8.08 inches of rain occurred in 24 hours at Beaufort West, which is the heaviest day's rain of the stations considered. This, it will be observed, is nearly the average for a year at this station. As much as 9.7 inches has been recorded in one month. An examination of table 4, giving rainfall extremes, will show that the maxima and the minima for the four seasons are all very well marked, the greatest possibly occurring in winter. Over a period of 43 years, two rainy spells of 5 days each were reported, which aggregated 2.98 inches. At Beaufort West there is an average of 16 rainy days during which less than 0.1 inch of rain fell. At Beaufort West, also, there are 3.1 months every year which constitute the drought period. During 1.3 months, taking the average of 43 years, no rainfall occurs at Beaufort West. The seasonal distribution of the drought, which is elsewhere defined, is: in summer 19.8, in autumn 13.9, in winter 40, and in spring 25.7 per cent. The actual seasonal precipitation at Beaufort West is 2.9 inches in summer, 3.4 inches in autumn, 0.9 inch in winter, and 2 inches in spring.

LAINGSBURG.

At Laingsburg the average rainfall is 4.47 inches, which is distributed through the year as follows: 19.9 per cent in summer, 35.8 per cent in autumn, 27.5 per cent in winter, and 16.5 per cent in spring. The actual rainfall for the four seasons in order as above given is: 0.8 inch, 1.6 inches, 1.2 inches, and 0.7 inch, from which it will appear that the most rain is in autumn and winter. This, however, is inconsiderable, and Laingsburg is one of the most arid stations of the Great Karroo.

The average yearly drought period at Laingsburg is 5.2 months, of which 34 per cent is in summer, 17 per cent each in autumn and winter, and 31.9 per cent in spring. As for the length of the average drought period, that at Laingsburg is exceeded by few stations in the Union, of which may be mentioned O'okiep and Upington. At Laingsburg, and for a period of observations covering 18 years, in 61 months no rainfall whatever was recorded, which is an average of 3.3 months yearly. Thus the average length of the rainless season at Laingsburg is approximately 2.4 times that of Beaufort West.

The number of days yearly during which 0.1 inch of rain falls at Laingsburg is 9.3, as compared with 16 at Beaufort West. The longest rainy spells at Laingsburg are of four days, of which two aggregating 1.62 inches precipitation have been reported.

As might be expected, the rainfall extremes at Laingsburg are very well marked. The maximum precipitation recorded for a year is 7.1 inches and the minimum precipitation is 1.06 inches. The maximum for summer is 2.8 inches, for winter 2.19 inches, and for spring 2 inches, with no precipitation, in each instance, as the opposite extreme. The maximum recorded for autumn is 4.36 inches, with 0.29 inch as the minimum. The maximum monthly rainfall reported for Laingsburg is 3.18 inches and the heaviest rain for 24 hours at Laingsburg is 1.75 inches.

MATJESFONTEIN.

The average annual rainfall at Matjesfontein is 6.8 inches, which is distributed through the year as follows: 17.8 per cent in summer, 33.3 per cent in autumn, 25 per cent in winter, and 23.6 per cent in spring. The actual amounts of rainfall are 1.1, 2.1, 1.6, and 1.5 inches for the four seasons, respectively. From this it will be seen that the rainfall at Matjesfontein resembles that of Laingsburg in distribution through the year, but is somewhat larger in amount. As at Laingsburg, the extremes in the reported amount of rainfall are very considerable; thus, the maximum yearly rainfall at Matjesfontein is 10.38 inches and the minimum 2.16 inches. The maximum rainfall of summer is 4.9, for autumn 6.1, for winter 5.1, and for spring 4.7 inches, with no rain for the opposite extreme. The greatest rainfall for a month is 3.3 inches¹ and in 24 hours 2.06 inches. At Matjesfontein, in 33 years, there has been one rainy spell of 5 days' duration, two of 6 days' duration, and one of 7 days, which is strongly opposed to the condition at Laingsburg, with no rainy period more than 4 days in length.

The length of the average yearly period of drought is 3.9 months, of which 35.3 per cent is in summer, 20 per cent is in autumn, 15.3 per cent is in winter, and 29.2 per cent is in spring. At Matjesfontein

¹ June 1921, 4.30 inches rain at Matjesfontein.

also there are on the average three months in which no rain occurs, from which it will be seen that the amount of rain falling in amounts of less than 0.15 inch in a month are relatively small, although there are on the average 18.8 days each year with less than 0.1 inch rainfall. As has already been pointed out, the average annual rainfall at Matjesfontein is 6.8 inches and that of Laingsburg is 4.4 inches. The average annual rainfall at the latter station is therefore 2.4 inches less than at the former station, although the two are but 18 miles apart.

TABLE 5.—*Drought periods (periods with less than 0.15 inch rainfall in a month).*

	Maximum length of continuous drought, in months.	Yearly average number separate continuous drought periods, 1 month or more each.	Total number drought periods, 1 month or longer. (Length of record years, in parenthesis.)
Cape Town.....	3	0.59	35 (59)
Grahamstown.....	2	0.18	8 (43)
Pietermaritzburg.....	3	0.92	24 (26)
Ladysmith.....	3	0.97	40 (39)
Montagu.....	4	1.50	56 (37)
Oudtshoorn.....	4	1.50	64 (42)
Uniondale.....	2	0.95	44 (42)
Aberdeen.....	4	1.80	71 (39)
Graaf Reinet.....	4	1.50	62 (40)
Beaufort West.....	5	2.10	94 (43)
Laingsburg.....	5	2.80	51 (18)
Matjesfontein.....	6	2.30	78 (23)
O'okiep.....	8	2.30	91 (38)
Upington.....	7	2.40	68 (28)
Pretoria.....	4	1.40	26 (18)
Pietersburg.....	6	1.30	23 (17)
Messina.....	7	1.50	17 (11)

The rainfall between these two stations is apparently graduated, decreasing in amount as one goes east toward Laingsburg. Going westward from Matjesfontein, the opposite condition obtains, the rainfall increasing in a marked manner in short distances. For example, for two years ending in June 1921, the total rainfall at Matjesfontein was 20.49 inches, while at a station 2 miles to the west it was 25.64 inches, at a second station 4 miles west it was 30.39 inches, at a third station 5 miles west it was 31.4 inches, and at a fourth station 7 miles west it was 33.78 inches. That is, in a horizontal distance of approximately 7 miles a total difference of rainfall in two years was found to be about 13 inches. Without entering into an account of the topography of the region immediately about Matjesfontein, which is touched on on another page, it can be said that while the altitude at Matjesfontein is 2,955 feet, that of the station 7 miles to the west is 3,585 feet, and that the hills both to the north and to the south are

nearer the western station. These differences in rainfall have a very striking effect on the kind and the amount of the vegetation, as will appear elsewhere.

DROUGHT PERIODS.

The length of the continuous drought periods, that is, the period (number of months) in a year either with no rainfall or with less than 0.15 inch of rain, is extremely variable as between the different stations, more especially in the arid regions of southern Africa. This can be illustrated by reference to the records for a few representative stations.

The least number of months with no rain, or with less than 0.15 inch of rain is at Grahamstown, where in 43 years only eight months are reported as being months of drought in the sense here understood. A drought period occurs about once in five years at Grahamstown. The maximum recorded length of a drought period at Grahamstown is about two months.

At Cape Town, the average yearly periods of drought in months are four times the length of those at Grahamstown. At the former the drought period is 0.23 and at the latter it is 0.93 month.

The maximum length of a drought period at Cape Town is about three months and at Pietermaritzburg it is about the same. These are the lowest maxima of any stations under discussion.

At Ladysmith, Montagu, Oudtshoorn, and Uniondale, in the Little Karroo, the maximum length of continuous drought periods are 3, 4, 4, and 2 months for these stations respectively. At the two former stations there are on the average about three drought periods in two years, and at the latter stations there is about one such period every year.

Of the stations in the Great Karroo, the maximum length of the drought periods is 4 months each at Aberdeen and Graaf Reinet, 5 months each at Beaufort West and Laingsburg, and at Matjesfontein it is 6 months. Of these stations the yearly average number of separate drought periods is least at Graaf Reinet, with the number at Aberdeen, Beaufort West, Matjesfontein, and Laingsburg successively larger. Thus, the order of the number of separate periods of drought for these stations is the converse of the annual rainfall occurring at them.

At O'okiep, observations covering 38 years, 91 separate drought periods have been reported, or an average of 2.3 each year. Of these there are one of 8, one of 6, four of 5, and two of 4 months duration. They are mainly in the warm seasons.

In 28 years, 68 drought periods were reported at Upington. There were two of 7 months duration, one of 6, five of 5, and three of 4 months. The greatest number of drought periods at Upington is in the cool seasons.

At Pretoria, in 18 years, there were 26 periods of drought, with four months as the maximum. At Pietersburg, during 17 years, the number of drought periods was 23 and the longest was 6 months. At the latter station there were four periods of 4 months, three of 5 months, and one of 6 months duration.

At Messina, in 11 years, there were 17 drought periods with 7 months as the longest. Of these there were two of 4 months, two of 5 months, two of 6 months, and one of 7 months duration. Messina, thus, with 14.5 inches rainfall, has somewhat larger drought expectancy than Pietersburg, or Pretoria, at which the rainfall is 21, 18, and 29.2 inches, respectively. But Pretoria, which thus has a larger rainfall than Pietersburg, has also a relatively larger number of drought periods, reversing the rule referred to in a preceding paragraph.

RAINFALL IN THE PROTECTORATE OF SOUTHWEST AFRICA AND IN THE NORTHWESTERN PART OF THE UNION.

A vast region stretches northward from the Great Karroo to and beyond the Tropic of Capricorn, reaching to the Atlantic Ocean, in which the rainfall is 10 inches, or less, annually. The amount of precipitation decreases from the south to the north, and from the west to the east. The exceptions to these generalizations occur in the Protectorate of Southwest Africa, where in the highlands there is higher rainfall, and in the extreme south of Cape Colony, in which, in part at least, for a similar reason, irregularities exist. In the Protectorate are to be found the most arid portions of South Africa, if not of the Southern Hemisphere, lying between the highlands and the ocean. It is the Namib Desert and its southern extension. Thus, at Luederitz Bay, the annual rainfall is given by Knox as 0.79 inch and Swakopmund 0.83 inch. In the highlands, however, the rainfall in places exceeds 20 inches.

The stations of which the rainfall will be especially spoken of in this review are O'okiep, in Namaqualand, south of the Orange River and distant in a straight line about 50 miles from the Atlantic Ocean, and Upington, on the Orange River, distant about 250 miles from the ocean, both of which are in the Union of South Africa, and the following stations in Great Namaqualand, or the Protectorate: Warmbad, about 120 miles from the ocean and about 50 miles north of the Orange River; Keetmanshoop, about 150 miles from the ocean and 50 miles north of Warmbad; Bethany and Gibeon, lying between Keetmanshoop and Windhoek; Windhoek, 160 miles, and Gobabis, about 250 miles, in a straight line from the Atlantic Ocean; Karibib, Swakopmund, and Luederitz Bay. Karibib is between Windhoek and Swakopmund, which is on the ocean. Luederitz Bay, about 250 miles south of Swakopmund, lies nearly west of Bethany and northwest of Keetmanshoop and about 500 miles north of Cape Town.

O'OKIEP.

The altitude above sea-level of O'okiep is 3,025 feet, of Upington is 2,641 feet, of Warmbad 2,361 feet, of Keetmanshoop 3,286 feet, of Gibeon 3,707 feet, of Windhoek 5,428 feet, of Gobabis 4,649 feet, of Karibib 3,842 feet, and that of Bethany not far from 3,500 feet.

The rainfall at O'okiep is 6.4 inches, the average of 38 years' records, distributed through the four seasons as follows: in summer, 0.6 inch; in autumn, 2 inches; in winter 2.6 inches; and in spring 1.2 inches. There thus occurs 9.3 per cent in summer, 31.2 per cent in autumn, 40.6 per cent in winter, and 18.7 per cent in spring. The extremes in rainfall at O'okiep are very well marked. The maximum yearly

rainfall is 11.7 and the minimum 2.46 inches. The rainfall maxima of summer, autumn, winter, and spring are 2.5, 6.04, 6.17, and 3.3 inches, and the seasonal rainfall minima are nothing in summer, 0.6 inch in autumn, 0.7 in winter, and 0.1 inch in spring. The maximal fall for one month was 3.49 inches, and the heaviest rainfall experienced in 24 hours was 2.05 inches. The drought period is 5.9 months yearly, of which no rainfall occurs in 1.6 months; 42 per cent of the drought period occurs in summer, 17.4 per cent in autumn, 9.6 in winter, and 30 per cent in spring. Thus O'okiep is within the region of winter rains. There are at O'okiep about 41 rainy days each year, of which the daily rainfall on 23 days is 0.1 inch and less, and on 8 days the rainfall is from 0.11 to 0.20 inch. This makes a very small average daily, about 0.1 inch, with a relatively large number of rainy days.

WARMBAD.

The average rainfall at Warmbad for 11 years is 3.62 inches. There are 34 rainy days in the year, making the average daily rainfall 0.16 inch. The maximum and the minimum yearly precipitation at Warmbad are 6.04 and 0.69 inches. Summarized monthly rainfall data, 1913-1920, show that there are two rainy periods and two dry periods in the year. The primary period of little rain is in early spring, September, when the average precipitation is 0.03 inch. The monthly rains then increase gradually in amount up to and including December, when 0.91 inch occurs. They are somewhat less in January, 0.35 inch, and then increase to the maximum in March, early autumn, when the average is 2.03. The monthly amount of precipitation decreases rapidly, so that in April the average is 0.47 inch and in May and June it is 0.08 inch. For the period 1913-1920, the yearly precipitation was 5.83 inches, distributed through the seasons as follows: 2.03 inches in summer, 2.58 inches in autumn, 0.56 inch in winter, and 0.66 inch in spring. Thus there is 34.8 per cent in summer, 44.3 per cent in autumn, 9.6 per cent in winter, and 11.1 per cent in spring. The heaviest rain of summer is in December, and the heaviest rainfall of the cool season in March.

KEETMANSHOOP.

At Keetmanshoop the average rainfall for the 11 years, 1908-1920, was 4.84 inches, the maximum being 8.6 and the minimum 1.2 inches. The average rainfall, however, for the years 1913 to 1920 was 6.43 inches. This was distributed through the seasons as follows: 3 inches in summer, 2.2 inches in autumn, 0.1 inch in winter, and 1.09 inches in spring. Thus, 46.6 per cent of the annual precipitation at Keetmanshoop occurred in summer, 34.9 per cent in autumn, 1.5 per cent in winter, and 16.9 per cent in spring.

BETHANY.

The average rainfall at Bethany, 1908–1920, was 3.9 inches. The maximum for that period was 9.6 and the minimum 1.18 inches. For the period 1913–1920 the average rainfall at Bethany was 5.43 inches. Of this, 2.7 inches occurred in summer, 1.8 inches in autumn, 0.1 inch in winter, and 0.77 inch in spring. Thus, 50 per cent of the rainfall is in summer, 33.4 per cent in autumn, 1.8 per cent in winter, and 14.3 per cent in spring.

GIBEON.

At Gibeon the average rainfall, 1908–1920, was 6.36 inches. The maximum was 14.35 and the minimum 2.21 inches. Of the period 1913–1920, the average annual rainfall was 7.7 inches, of which 4.11 inches was in summer, 2.69 inches in autumn, 0.11 in winter, and 0.79 in spring; from which it will be seen that 53.3 per cent of the yearly rainfall occurs in summer, 34.8 per cent in autumn, 1.4 per cent in winter, and 10.2 per cent in spring. There is thus a relatively small amount of rain in winter, as in the last two stations especially, and a relatively large proportion in the warmer seasons.

WINDHOEK.

At Windhoek the average rainfall for the period 1908–1920 was 13.37 inches, the maximum 22.45, and the minimum 5.7 inches. For the period 1913–1920 the average annual rainfall was 14.67 inches. It was distributed as follows: 8.89 inches in summer, 4.2 inches in autumn, 0.02 inch in winter, and 1.56 inches in spring. From this it will be seen that 60.59 per cent occurs in winter, 28.6 per cent in autumn, 0.13 per cent in winter, and 10.6 per cent in spring.

GOBABIS.

At Gobabis, for the period 1908–1920, the average rainfall was 15.53 inches. The maximum rainfall for the period was 26.6. The average rainfall at Gobabis for the period 1913–1920 was 15.48 inches, which was distributed through the seasons as follows: 9.24 inches in summer, 4.51 inches in autumn, no rainfall in winter, and 1.72 inches in spring. From this it will be seen that in summer there occurs 59.6 per cent, in autumn 29.1 per cent, and in spring 11.1 per cent.

KARIBIB.

The average rainfall at Karibib for 1908–1920 was 7.38 inches. The rainfall extremes for this period were 12.49 and 2.62 inches. For the period 1913–1920, the average annual rainfall at Karibib was 8.71 inches, of which 5.09 inches occurred in summer, 2.75 inches in autumn, there was no rainfall in winter, and in spring 0.87 inch. Therefore 58.4 per cent of the rainfall at Karabib occurs in summer, 31.5 per cent in autumn, and 10 per cent in spring.

SWAKOPMUND.

At Swakopmund for the period 1908-1920 the average annual rainfall was 0.69 inch. The maximum rainfall for this period was 2.41 inches and the minimum was 0.01 inch. For the period 1913-1920 the average annual rainfall was 1.02 inch, of which 0.72 inch was in summer, 0.18 inch in autumn, no rain in winter, and 0.12 inch in spring. From this it will appear that while the rainfall at Swakopmund is very small indeed, it mainly occurs in the warm season, that is, at the time of the heaviest rains in the highlands to the east. February is the most rainy month.

LUEDERITZ BAY.

The average rainfall for the period 1908-1920 at Leuderitz Bay was 1.97 inches. The maximum rainfall for a year was 4.31 inches and the minimum 0.67 inch. Of the period 1913-1920 the average rainfall was 2.95 inches, of which 0.93 inch occurred in summer, 0.54 inch in autumn, 1.27 inches in winter, and 0.21 inch in spring. From this it will be seen that the rains of summer are 31.5 per cent, of autumn 18.1 per cent, of winter 43 per cent, and of spring 7.1 per cent.

The average number of rainy days for the period 1908-1920, 11 years, at the Protectorate stations given above, varies from 29 to 70. Warmbad and Luederitz Bay have the least and Gobabis the largest number of rainy days per year. At Keetmanshoop the number was 36 and at Bethany it was 30, at Gibeon it was 46, at Windhoek 66, at Karibib 43, and at Swakopmund 50. The average amount of rainfall per rainy day varied from Swakopmund with 0.01 and Luederitz Bay with 0.06 inch, to Gobabis with 0.22 inch. At Grootfontein, however, which is about 200 miles north of Windhoek and about 350 miles from the coast, the rainfall is 20.34 inches, with 77 rainy days. Period 1908-1920, the daily average precipitation on rainy days, therefore, is 0.26 inch. But the heaviest average rainfall of the Protectorate is Omapunda with 607 mm., or 23.9 inches.

DROUGHT PERIODS IN THE PROTECTORATE.

The drought periods, that is, the number of months without precipitation or with less than 0.15 inch, constitutes a very prominent characteristic of the climatic conditions of the Protectorate. The following remarks on the subject are taken from records covering the period 1913-1920. In this period Grootfontein and Gobabis had each 28 months of drought, which was the least drought aggregate, and at Swakopmund the number of months with drought was 47, the largest drought aggregate. Owing to the occurrence of rains for the most part in the warm seasons, the drought periods are mainly in the colder seasons, especially in winter. At Windhoek, Gobabis, Karibib, and Grootfontein there is no drought in summer, but from 50 to 64 per cent

of the drought is in winter. At the other stations mentioned above the drought in winter is from 23 to 48.4 per cent, increasing from the south to the north. Thus at Luederitz Bay the percentage of winter drought is 23, at Warmbad it is 26.4, at Keetmanshoop it is 46.8, at Bethany it is 45.4, and Gibeon 48.6, with 52.1 per cent and more at Karibib and other stations as mentioned above. At Swakopmund the percentage of winter drought is 31.8. At both Swakopmund and Luederitz Bay about 15 per cent of the drought periods occur in summer. The drought in a single continuous period is naturally often considerable, varying between 5 and 9, and possibly more. At Swakopmund, during the period 1913-1920, in three years in which the complete records are at hand, there were 9 months of continuous drought, that is, with less than 0.15 inch rainfall per month, with an annual average drought aggregate of 9.5 months. It will be rightly concluded, from what has been said above, that the seasons of drought include winter and do not include summer, but may include months from autumn or spring.

EFFECTIVE PRECIPITATION.

As stated elsewhere, the special features characteristic of rainfall in arid regions are not only the small amount and its variations from season to season, but also the possibly great differences in the amount of separate storms. The circumstance last referred to is of some ecological importance.

In arid regions two classes of precipitation are of little direct value to vegetation, namely, heavy rains of short duration, on the one hand, and inconsequential showers on the other. In the former the rains fail to moisten the soil deeply because of rapid run-off, and in the latter case because they are of too small amount. The possible indirect effect of such types of rain, especially of that last named, is not here considered, inasmuch as in the long run the vegetation of an arid region is dependent on the moisture of the soil for its water-supply.

For the purpose of defining the amount of rainfall directly beneficial to vegetation in an arid region, and in this case cloudbursts and the like are not taken into consideration, the effective rainfall has been arbitrarily taken as consisting of 0.15 inch or more, which occurs in a single stormy period.¹ Amounts under 0.15 inch are considered to be non-effective. The effective rainfall is derived by subtracting the total non-effective rainfall from the precipitation.

In table 6 are given the mean annual precipitation, 1913-1922 (P), and the mean annual effective (E) and non-effective (N-E) precipitation, together with ratios based on the same. In the last column are given maximal ratios of effective and non-effective ratios for the period.

¹ Plant habits and plant habitats in the arid portions of South Australia. W. A. Cannon. Carnegie Inst. Wash. Pub. No. 308, p. 48, 1921.

The data appear to indicate that there is a relation between the seasonal distribution of the rainfall and the relative amount that is effective. Thus, in regions of summer rains the effective precipitation is relatively large, but, on the other hand, in regions of winter rains it may be relatively small.

TABLE 6.—Mean annual precipitation (*P*); mean effective (*E*), and mean non-effective (*N-E*) precipitation, with *E/P* and *N-E/P*, and maximum *N-E/E* ratios, 1913-1922.^a

	P., in.	E., in.	N-E., in.	Per cent mean E/P.	Per cent mean N-E/P.	Per cent maximum N-E/E.
Cape Town.....	26.39	23.47	2.92	89	11	16
Grahamstown.....	29.87	26.52	3.35	89	11	18
Pietermaritzburg....	44.51	40.20	4.24	90	10	15
Montagu.....	13.62	12.35	1.27	90	10	19
Ladysmith, C. P....	15.83	14.69	1.14	92	8	20
Oudtshoorn.....	11.83	10.44	1.39	88	12	22
Uniondale.....	14.45	12.46	1.99	86	14	27
Matjesfontein.....	9.08	8.0	1.08	88	12	27
Laingsburg.....	5.36	4.75	0.61	89	11	27
Beaufort West.....	12.50	10.85	1.65	87	13	29
Graaf Reinet.....	15.41	13.85	1.56	90	10	21
Aberdeen.....	13.35	12.14	1.21	91	9	22
Upington.....	7.43	6.56	0.86	88	12	17
O'okiep.....	8.95	7.49	1.46	84	16	25
Pretoria.....	31.84	29.43	2.41	92	8	9
Pietersburg.....	23.09	21.82	1.67	94	6	13

^a Based on data supplied by the Meteorological Office, Pretoria.

It is likely that in regions either with rain in summer or in winter, the region having the larger amount has also relatively more effective rain than the one having a small amount. For example, the precipitation at Beaufort West is 9.46 inches and at Graaf Reinet it is 13.98 inches. In the former place 65 per cent occurs in summer and in the latter 66 per cent. At Beaufort West the precipitation is 87 per cent and at Graaf Reinet it is 90 per cent effective. It is as if the former station had a rainfall of 8.2 inches and the latter a rainfall of 12.5 inches, both being equally effective. Beaufort West, consequently, is somewhat more arid, in reference to the rainfall only, as compared with Graaf Reinet, than would be indicated by the precipitation at the two stations only.

The mean relative effectiveness of the rainfall is surprisingly high, taken as a whole. In the Karroos, for example, it ranges between 86 and 92 per cent. Even at Laingsburg, where the annual precipitation is extremely low, it is about 89 per cent effective. About 52 per cent of the rainfall at this place is in summer.

The extreme differences between the effective and the non-effective rainfall for a year at one place indicate that occasionally there may be years in which, owing to the large total amount of the latter, the moisture available to the use of plants is markedly below the supposed

amount as indicated by the precipitation taken altogether. This feature is brought out in the last column of table 6. It will be seen that from 27 to 29 per cent of the rainfall in the Karroos for a year may be non-effective. It is so great moisture deficiency in unusually dry years or seasons, occasioned in part by relatively large proportion of non-effective precipitation, that may turn the scales in determining the suitability of a species for a given habitat. In effective-noneffective rainfall extremes, as in the means, where the rainfall is relatively large, the non-effective rainfall is relatively small, and of a consequence there is an increase in aridity out of proportion to possible differences in total precipitation.

Such considerations as briefly presented above indicate that in comparing one region with another on the basis of precipitation, particularly if the regions are arid, account should be taken of the amount of rain that occurs in small amounts, but which nevertheless may be an important percentage of the rainfall taken as a whole.

MOISTURE OF THE AIR.

SEASONAL VARIATION IN RELATIVE HUMIDITY.

The annual course of the relative humidity follows that of the rainfall, and is not necessarily the converse of that of the temperature, as frequently is the case. And, according to Cox,¹ "although the amount of water-vapour in the air decreases from the coast inland the north-easterly and easterly winds of the summer months convey to the high veld more moisture than is probably present on the same plane at the coast." Possibly an analogous condition may obtain in winter as regards the western coast and contiguous interior regions.

The annual range of the mean relative humidity may be considerable. Thus at Johannesburg, which does not appear to be extreme in this regard, it ranges from 49 per cent in September to 75 per cent in April, according to Knox. During the months of August, October, and November, the mean relative humidity is 54 to 58 per cent; in the months of summer it is 60 to 70 per cent; in autumn it is 71 to 75 per cent; and 67 to 69 per cent in June and July. At Table Bay the mean minimum is 67 per cent and occurs in December and January, and the mean maximum is in May to August, when it lies between 80 and 81 per cent. From November to March the mean relative humidity is between 67 and 69 per cent. It is 74 per cent in April and from 73 to 77 per cent in September and October.

As compared to the conditions which obtain at Table Bay, the climate at Clanwilliam, especially the relative humidity, has certain points of interest. Thus, at Clanwilliam, which lies about 40 miles

¹ A guide to botanical survey work. Botanical survey of South Africa, Mem. No. 4, p. 28. 1922.

from the western coast and about 130 miles north of Cape Town, the annual rainfall is 8.57 inches, of which about 79 per cent is in winter. The mean annual relative humidity is 76 per cent as opposed to the mean annual relative humidity at Table Bay of 74 per cent. The annual rainfall at the latter place, which also occurs mostly in the cool seasons, is approximately three times as great as at Clanwilliam. The yearly extremes in the mean relative humidity at Clanwilliam are from 61 per cent in December to 89 per cent in August.

In the eastern portion of the Central Karroo, at Graaf Reinet, the mean annual relative humidity is 65 per cent. The mean monthly minimum is 57 per cent and occurs in July, and the mean maximum is 73 per cent in February. From August to January the mean relative humidity ranges from 60 to 68 per cent and falls to 64 per cent for June. Graaf Reinet is under the influence of the summer rains.

At Kimberley, on the northern border, the range in the mean monthly relative humidity is from 46 per cent in November to 66 per cent in April and June. The mean annual relative humidity is 56 per cent.

Calvinia, in the upper Karroo, which is about 80 miles from the west coast and about 200 miles from the south coast, has a climatic environment fairly like that of the western portion of the Karroo.¹ Here the mean relative humidity of winter lies between 60 and 70 per cent and in the other months between 50 and 60 per cent.

At Oudtshoorn, in the Little Karroo, according to Dove, the mean annual relative humidity is 76 per cent. The mean monthly minimum is in February, 69 per cent, and the mean monthly maximum, 82 per cent, is in May. From September to January the mean monthly relative humidity runs between 70 and 76 per cent. In March and April it is 76 and 79 per cent, and May-August it is 82 to 80 per cent.

At O'okiep, in the Namaqualand desert province, according to Marloth,² the mean annual relative humidity is 48 per cent; the mean monthly minimum is 40 per cent, November-December, and the mean maximum is 58 per cent, in July. From April to August the mean monthly humidity ranges between 52 and 58 per cent, and between 40 and 48 during the other months.

Data on the relative humidity for other stations of the Namaqualand desert province are apparently meager. Dove (*l. c.*) gives that at Hope Mine, which is 100 km. southeast of Walfisch Bay and 80 km. from the coast, as 44 per cent from January 18 to March 21. At Ni-Guib, from June to September, it was 50 per cent. During the middle of the day the humidity fell to 31 per cent at Hope Mine and 26 per cent at Ni-Guib.

¹ Das Klima des aussertropischen Südafrika. K. Dove, 1888, p. 51.

² Das Kapland, *q. v.*, p. 36.

WINDS.

The direction, force, frequency, and duration of winds are very important elements in the environment of plants, particularly in arid or semi-arid regions. Du Toit,¹ speaking of the work of the atmosphere as a geologic agent, with especial reference to wind action, says that loess is being formed "along the intermittent rivers and on the lee sides of pans in northern Cape Province, for even a slight breeze is usually sufficient to raise clouds of fine dust from the dried mud which composes the floors of these depressions."

The formation of sand-dunes is of fairly frequent occurrence in certain regions both along the coast and in the interior. They constitute a prominent character of the physiography along the coast at Swakopmund and southward as well as to the north. Along the Clanwilliam coast the coarser wind-blown sand makes thick deposits, obliterating many smaller features of the surface. In the interior Du Toit says that the accumulation of the sand into dunes in places retains a height of about 100 feet and there is a long succession of sandhills. He mentions how the channel of the Molopo River, which drains a portion of the Kalahari, has been choked by sand so that on the rare occurrence of water in the river it is deflected from its proper course to make its way through sandhills, where it disappears. Along river banks there frequently occur sandy stretches which derive the sand from river-beds, when dry, through wind action. Some of these accumulations attain a height of 40 feet. In southern Algeria sand is strewn in a similar manner along and near stream-ways, forming a mulch which serves to better conserve the small amount of moisture in the soil, as is evidenced by the relatively abundant plant population of such areas.²

The winds, especially in arid regions, are often important agents of erosion through the polishing and grinding action of the sand which they carry. In the Libyan Desert pebbles of good size are thus transported. Often the rock surfaces exposed to the erosive action of the sand-carrying winds are polished or worn away, especially near the ground, leaving the upper or harder portions. The exposed surfaces of small stones, also, may be polished or flattened, as in the case of the "gibbers" of vast gibber-plains in northern South Australia.³ Although similar action must be in progress in South Africa, it is not of sufficient importance to be mentioned by Du Toit.

The direction of the prevailing winds in different portions of southern Africa changes with the seasons, although in certain stations the winds appear to be fairly constant, on the whole, as to the general direction.

¹ Physical Geography of South African Schools, Cambridge, p. 67, 1921.

² Botanical features of the Algerian Sahara. W. A. Cannon. Carnegie Inst. Wash. Pub. No. 178, 1913.

³ Plant habits and habitats in the arid portions of South Australia. W. A. Cannon. Carnegie Inst. Wash. Pub. No. 308, 1921.

In portions of Southwest Africa, as at Omaruru, according to Dove (*l. c.*), in the warm seasons the winds are mainly from the northeast quadrant, while in the cool seasons they are mainly from the southwest-northwest quadrant. The former bring the summer rains.

At Graaf Reinet, in the Central Karroo, out of 696 observations it was found that in the warm season the winds came mainly from the southeast and in the cool season mainly from the northwest. At Aliwal North, in the warmer seasons the winds are mainly southeasterly, while winter appears to be largely a season of calm. At Grahamstown the prevailing winds, both of the warmer and of the colder seasons, are from the southwest, although in the warmer seasons there is a large proportion of southeasterly winds, and in the colder seasons a large proportion of winds from the west. Under proper conditions the moisture in such winds is precipitated as rain. Where such is not the case they nevertheless may directly affect vegetation through raising the humidity, as was frequently observed in the Karroo in early spring. On the Namib, too, the sea-breeze brings inland heavy fog, and at Swakopmund and elsewhere on the Namib the moisture of such winds may be deposited like dew. Thus Pearson¹ says:

“Other features of this most interesting desert-region, the Namib, which force themselves upon the notice of the traveller are the mirage and the night fogs The night fogs in so arid a region are hardly less remarkable. About 8 o'clock in the evening of January 24, as we crossed the dry bed of Tubas River, a cloud appeared in the west. The stars were gradually obliterated, and by 10 o'clock we were shrouded in a cold ‘Scotch mist.’ After sleeping on the ground from midnight until 4 o'clock on the following morning I was able to wring the water out of my top-covering, a woollen rug. As soon as daylight came, the ground was seen to be discoloured by the moisture absorbed, and the plants were copiously sprinkled with dew. At 7 a. m., on January 30, the water was dripping from the branches of the Tamarisks in the Khan valley at Haikamchab.”

The fog drifts inland with the sea-breeze to a depth of 30 miles, more or less.

When the east wind blows on the Namib there is neither fog nor dew, and intensely arid conditions obtain. According to Knox, winds of this kind are characteristic of the west coast to the north of Clanwilliam.

MacDougal² states that in portions of the Libyan Desert the lack of vegetation may not—

“ultimately be due to lack of water but to wind-action. Plants are found in innumerable places in which the supply is no greater than that of the bare areas, but in exposed places the surface layers of sand and gravel are shifted about, exercising a corrosive action that is destructive to plants and highly

¹ Some notes on a journey from Walfisch Bay to Windhuk. H. H. W. Pearson. *Bul. Misc. Information*, No. 9, 1907, Roy. Bot. Gar., Kew, p. 349.

² The deserts of western Egypt. *Plant World*, vol. 16, 1913, p. 303.

important in determining the contours of hills and the surface of rocks. Highly specialized 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 annual and the slowly growing leathery xerophytes."

The character of the winds referred to in the preceding paragraphs are of a general nature, extending over wide areas, and may largely be associated with far-extending atmospheric disturbances, such as general rains. They, moreover, may be, and frequently are, of considerable force, whether moisture-bearing or otherwise. There is, however, quite another type which is also of importance to plant life in arid regions, and which are not referred to in meteorological reports. Such are purely local winds, which may be extremely variable as to direction, duration, force, and capacity of giving out or of taking up moisture. Often these are little more than convection air-currents, but which notwithstanding this may be important in modifying the relative humidity and the temperature and in this manner more especially directly affect plant life. Whatever may be the origin of such winds, they are practically always to be found in arid regions, where they are especially noticeable because of the paucity of cover. At Beaufort West and Matjesfontein it was often noted that however calm the veld was in early morning the breezes began with the rising of the sun and seldom stopped through the day. When such winds came from higher and more humid elevations they notably increased the relative humidity. This was noticed at Matjesfontein in September, in connection with winds from the south and southeast, and which were of local origin. When, however, they came from the opposite direction, the humidity of the air was maintained very low, so that in working with cobalt-chloride papers in studying the transpiration of certain plants, the papers remained dark blue even when exposed to the air, when under other conditions they would quickly assume a pink color. Such winds also were found to have a noteworthy effect on the rate of evaporation, as shown by the readings of the atmometers, circumstances that will be spoken of in another place.

EVAPORATION.

Investigations on evaporation in southern Africa have proceeded along two lines. They either have had to do with the amount of water lost from a free water-surface or the amount lost from the moist surface of a porous clay cup or atmometer. The former extend over a fairly long period and for the most part have been carried on by the meteorological bureau of the government, while the latter, on the other hand, begun by volunteer observers, are being taken up by the Botanical Survey of South Africa, and cover but a short period of

time. Their immediate aim is to define, so far as possible, the evaporating power of the air as an environmental factor of plants.

At Kimberley, according to Twigg¹ the evaporimeter consisted of a wrought-iron tank 4 by 4 by 4 feet in size, sunk in the ground within 1 inch of the surface and kept full of water. The mean evaporation was 86.68 inches and the highest was 104.39 inches. The least monthly mean, 4.3 inches, was in June, and the greatest, 12.1 inches, in December. From April to August, inclusive, the monthly mean was between 4.3 inches and 6.4 inches. From October to January it was between 10.8 inches (October), and 12.1 inches. The rate decreased month by month from January to June, when it increased steadily until the end of the year.

With the use of the type of apparatus above referred to, it was found that in 1894 the evaporation was 91.26 inches, and in 1895 it was 101.84 inches. From 1894 until 1900 another type of free water-surface evaporimeter was employed at Kimberley which gave a mean of 90.1 inches for this period. In 1894, by the later apparatus, it was 77.93 inches, and in 1895, 88.43 inches, which will be seen to be somewhat less for the two years than was found to be the case with the earlier type of evaporimeter employed.

At Kimberley, in the year 1900, a comparative study was carried out of four different types of evaporimeters, the results of which need only be referred to in this place. The use of an 8-inch copper pan gave 90.82 inches, a screened tub gave 61.98 inches, a tank gave 55.21 inches, and a Piche tube gave 82.83 inches.

Cox gives the annual evaporation at Johannesburg, the sum of the monthly means, as 74.67 inches, and at Cape Town as 78.57 inches. The least monthly evaporation at the latter is 4.35 inches and at the former 2.48 inches, both in June. At Johannesburg the highest monthly mean is 8.41 in October and at Cape Town 10.39 in January. The seasonal fluctuation of evaporation is greater also at Cape Town than at Johannesburg. Thus, in summer, at Cape Town, the evaporation is 30.2 and at Johannesburg it is 19.5 inches, and in autumn for the two stations respectively it is 18.01 and 15.2 inches. In winter it is 9.6 and 15.86 inches. In spring the evaporation at Cape Town is 20.7 and at Johannesburg it is 23.95 inches. At Cape Town 77 per cent of the rainfall is in winter and at Johannesburg 87 per cent of the rainfall is in summer. It will be of interest to compare the above seasonal evaporation means at Cape Town and Johannesburg with that at Kimberley. Thus, at Kimberley the mean evaporation for summer, autumn, winter, and spring is 32, 19.5, 15.5, and 30.1 inches. At Kimberley 78 per cent of the rainfall is in summer. The mean summer temperature at Kimberley is 75.86° F., at Cape

¹ Quarterly Journ. Roy. Soc. Met. Sci., vol. 22, p. 166, referred to by Sutton. Trans. So. African Phil. Soc., vol. 14, pt. 1, 1902.

Town it is 68.2°, and at Johannesburg it is 63.46° F. There appears thus to be a direct relation between the summer temperature at these three stations and the mean evaporation for the same season. This is of some interest, in view of the fact that summer is the season of greatest rainfall at Kimberley and Johannesburg and the least rainfall at Cape Town, as above stated.

RATIO OF RAINFALL TO EVAPORATION (P/E).

The precipitation-evaporation ratio is a convenient way of comparing stations of different regions, as well as different seasons at one station, as to the relation of rainfall to water-lost through the evaporating power of the air, for the station or for the seasons. The ratio is said by Livingston and Shreve¹ to be "the nearest approach that is yet possible toward an ideal index of the external moisture relations of plants," and as a general expression of the amount of water available to vegetation it is of great use.

The data at hand do not permit a satisfactory discussion of the P/E for South Africa, so that this index can not be charted as isoropic lines for geographical uses. However, some account can be presented of the precipitation-evaporation for Cape Town, Kimberley, and Johannesburg, representing the region of winter and of summer rainfall. The P/E of the three stations is shown graphically in figure 8. The high evaporation-rate in summer at Cape Town, as compared to the rainfall for the season, forms a marked contrast to the condition obtaining at Kimberley, and especially at Johannesburg, where, owing to the large summer precipitation, the evaporation-rate is relatively low. At Johannesburg, in January, the rainfall equals the evaporation, but in the balance of the year it is less. At Kimberley it is always less than the evaporation, and at Cape Town, for the three winter months, the rainfall is much in excess. The violent seasonal contrast in the external moisture relations of the plants at each of the three stations, particularly at Cape Town and at Johannesburg, are also strikingly shown in the graph.

ATMOMETRY IN SOUTHERN AFRICA.

The type of evaporimeter used in obtaining the results mentioned in the preceding paragraphs does not appear to be well suited for intensive studies on evaporation as one of the important physical factors of the environment, and it was decided to introduce the spherical atmometer as developed by Livingston.² Accordingly

¹ The distribution of vegetation in the United States, as related to climatic conditions. Carnegie Inst. Wash. Pub. No. 284, p. 326, 1921.

² Atmometry and the atmometer. Plant World, vol. 18, p. 148, 1915.

atmometers were placed at certain representative stations, named below, and were read by volunteer observers.¹

The work here reported must be considered introductory, merely, and conclusions based on it are tentative. The results to be given are taken directly from the field-books, for the reason that at the time of the visit there was no means of restandardizing the instruments, and further, because for the most part they deal with relatively short periods. As time went on, however, as the accompanying note intimates, there was increasing need of the restandardization in most instances. The records for Grahamstown and Matjesfontein, however, which are of much importance, are apparently satisfactory.

In the preliminary studies the atmometers were placed and read at the following stations: Messina and Pretoria, Transvaal; Pietermaritzburg, Natal; Grahamstown, Cape Town, Beaufort West, and Matjesfontein, Cape of Good Hope; Swakopmund, Protectorate of Southwest Africa. Messina is situated in the Low Veld, Pretoria on the northern edge of the High Veld, Pietermaritzburg in the Eastern Grass Veld, Grahamstown fairly between the latter and the Cape region, Beaufort West and Matjesfontein in the Karroo Province, and Swakopmund in Namaqualand Desert Province.

NATIONAL BOTANIC GARDENS.

At the National Botanical Gardens, Kirstenbosch, the atmometer was placed on the north slope, 6 feet above the ground, at an altitude of about 350 feet above sea-level, with other meteorological instruments.

The records at hand are for one year. Some difficulty was experienced from the flooding of the reservoir, owing to the faulty functioning of the valves used, so that the record is not complete. Table 7 gives the weekly evaporation for the period, less the gaps referred to. It is given in its entirety for the reason that it is the only long atmometer record at hand covering the region with winter rains.

Owing to the lack of completeness, without reference to possible instrumental errors, only general conclusions can be drawn from the gardens' record. So far as can be told, the monthly evaporation for the period in question varied from about 572 c. c. in September to about 1,012 c. c. in February, although the minimum amount might well have been less. The entire evaporation for spring was 2,373 as compared to an evaporation of 2,872 for the following summer.

¹ Such was the status while the writer was in South Africa. Upon his leaving, however, the Botanical Survey took over the work and at present it is being conducted for the Survey by Mr. R. D. Aitken, Natal University College, Pietermaritzburg. Mr. Aitken restandardized the atmometers above referred to about November 25, 1922, or before that date, and has kindly supplied revised coefficients for them as follows: Grahamstown, 0.90 to 0.88; National Botanical Gardens, Kirstenbosch, very variable, 0.90 to 1.51; Matjesfontein, 0.91; Pretoria, badly altered, 1.32 to 1.62.

About 2,131 c. c. of water-loss occurred in autumn and approximately one-half that amount in winter. The seasonal range in evaporation at Kirstenbosch is, therefore, very considerable. It is apparent that the amount of evaporation in the warm seasons, for the period con-

TABLE 7.—Weekly evaporation at the National Botanic Gardens, Kirstenbosch, August 15, 1921, to September 29, 1922.

Period of observation.	Water loss.	Period of observation.	Water loss.
1921.	c.c.	1922.	c.c.
Aug. 15 to 22.....	90	Feb. 11 to 17.....	218
Aug. 23 to 29.....	192	Feb. 18 to 24.....	215
* * * * ^a		Feb. 25 to Mar. 4.....	256
Sept. 16 to 24.....	133	Mar. 5 to 11.....	231
* * * *		Mar. 12 to 17.....	188
Oct. 14 to 21.....	168	Mar. 18 to 24.....	124
Oct. 22 to 28.....	203	Mar. 25 to Apr. 1.....	115
Oct. 29 to Nov. 5.....	250	Apr. 2 to 8.....	330
Nov. 6 to 11.....	250	Apr. 9 to 14.....	41
Nov. 12 to 18.....	157	Apr. 15 to 21.....	166
Nov. 19 to 25.....	220	Apr. 22 to 28.....	154
Nov. 26 to Dec. 2.....	237	Apr. 29 to May 13.....	315
Dec. 3 to 9.....	298	May 14 to 20.....	174
Dec. 10 to 17.....	180	May 21 to 26.....	37
Dec. 18 to 24.....	251	May 27 to June 2.....	122
Dec. 25 to 30.....	141	* * * *	
1922.		July 7 to 14.....	168
Dec. 30 to Jan. 6.....	334	July 15 to 21.....	239
Jan. 7 to 13.....	167	July 22 to 28.....	87
Jan. 14 to 20.....	105	* * * *	
Jan. 21 to 27.....	215	Sept. 9 to 16.....	58
Jan. 28 to Feb. 3.....	157	Sept. 17 to 23.....	114
Feb. 4 to 10.....	242	Sept. 24 to 29.....	133

^a The asterisks denote lack of record from flooding of reservoir.

TABLE 8.—Current and normal precipitation-evaporation ratios (P/E) at the National Botanical Gardens, 1921-22, with current and normal rainfall for Wynberg.

	P/E 1921-22.	P/E normal.	Rainfall Wynberg, 1921-22.	Rainfall Wynberg, normal.	Evapora- tion.
			inches.	inches.	c. c.
June.....	0.0284	0.0160	11.31	6.47	398
July.....	.0100	.0153	5.26	7.70	508
Aug.....	.0403	.0403	6.67	^a 6.67	163
Sept.....	.0066	.0075	3.82	4.31	572
Oct.....	.0034	.0027	2.58	2.03	742
Nov.....	.0009	.0013	0.86	1.26	959
Dec.....	.0011	.0010	1.06	0.95	931
Jan.....	.0018	.0005	1.71	0.48	929
Feb.....	.0006	.0005	0.63	0.53	1,012
Mar.....	.0002	.0024	0.13	1.75	714
Apr.....	.0021	.0034	1.83	2.93	861
May.....	.0062	.0110	2.99	5.52	476

^a Normal rainfall for August.

sidered, was approximately 62 per cent of the whole, or not far from twice that of the cool seasons.

It would be desirable to present the precipitation-evaporation ratio for the gardens for the seasons and the months covered by the records, only unfortunately, as this is written, there are no Kirstenbosch rainfall records at hand. However, an approximation will be made by substituting the records of precipitation for Wynberg, which is about 3 miles distant. In this the normal rainfall at Wynberg, as well as that for the particular months in question, will be used. A summary of the results are given in table 8.

It will be seen that the normal monthly values of the P/E and those for the particular month are very unlike. The normal extremes are 0.0005 and 0.016, while the current extremes are 0.00018 and 0.0284. The tentative mean monthly indices obtained by dividing the seasonal total by 3 are: summer, 0.0011; autumn, 0.0028; winter, 0.014; spring, 0.0036. The order of the relative aridity of the seasons are, therefore, winter, spring, autumn, and summer.

GRAHAMSTOWN.

At Grahamstown the atmometer records at hand are from June 23 to November 3, 1921. The atmometer was placed in a yard somewhat sheltered from winds, but exposed to the sun throughout the day. The altitude is about 1,350 feet above sea-level. The period of observation includes all of winter and the first month of spring.

As shown elsewhere, Grahamstown is fairly intermediate between the region of summer rains and the region of winter rains, with the effect that the precipitation is not markedly periodic, but approaches equal distribution through the year. In winter 39 per cent of the annual rainfall occurs. It increases to a primary maximum in spring and there is a secondary maximum in autumn.

It seems not improbable that the general distribution of the rainfall will be found to be reflected in the precipitation-evaporation ratio for the station, as is suggested by the meager data at hand. The actual water-loss, for a week, ranged between 119.5 c. c. for the week ended September 8 and 261.2 c. c. for the week ended June 30. The total monthly evaporation was as follows: July, 920 c. c.; August, 960 c. c.; September, 1,207 c. c.; October, 808 c. c. The normal annual rainfall for July is 0.67 inch, for August 1.08 inches, for September 3.28 inches, and for October 3.1 inches. From this it will be seen that the normal P/E ratio for July is 0.00072; for August it is 0.0010; for September it is 0.0027, and for October it is 0.0038.

The normal rainfall for July, August, and September is greater at Wynberg than at Grahamstown, but the October rainfall at Grahams-town exceeds that at Wynberg. The relative aridity for July, August, and September is apparently greater at Grahamstown, but the con-

verse appears to be true for October, as would be expected from the rainfall records and as is indicated by the P/E ratios. A comparison of the precipitation-evaporation indices based on the current rainfall might give even more striking results.

PIETERMARITZBURG.

At Pietermaritzburg, altitude 2,218 feet above the sea, the atmometer was placed on the roof of University College. The records at hand are from the week ending August 16, 1921, to the week ending February 28, 1922. They thus include the last month of winter and spring, and nearly two months of summer.

TABLE 9.—*Precipitation-evaporation ratios (P/E) at Pietermaritzburg, October 1921 to February 1922.*

[Normal rainfall and current rainfall in inches; evaporation in cubic centimeters.]

	Evapora- tion.	Rainfall, normal.	P/E, normal.	Rainfall, 1921-22.	P/E, 1921-22.
	<i>c. c.</i>	<i>inches.</i>		<i>inches.</i>	
Oct.....	1,077	3.14	0.0029	3.94	0.0036
Nov.....	884	4.08	.0046	6.34	.0071
Dec.....	1,016	5.04	.0049	9.05	.0088
Jan.....	1,313	5.21	.0039	2.41	.0018
Feb.....	1,235	5.06	.0040	2.33	.0018

The weekly amount of evaporation ranged from 168 c. c., for the week ending November 29 to more than 330 c. c., for the week ending September 20. The monthly totals for the period are: October, 1,077 c. c.; November, 884 c. c.; December, 1,016 c. c.; January, 1,313 c. c.; and February, 1,235 c. c.

The normal precipitation-evaporation ratio and the P/E are given in table 9, from which it will appear that the least normal P/E ratio is 0.0029 for October, and that the greatest is 0.0049 and is for December. The current ratios, on the other hand, are least in January and February and greatest in December, and on the whole correspond but poorly with the normal ratios. The difference is clearly related to the departure from the normal of the rainfall for the months in question.

MATJESFONTEIN.

At Matjesfontein, altitude 2,953 feet, the atmometer was placed on a fence in a yard which was somewhat protected from the southerly winds. It was exposed to the sun throughout the day.

The records at hand are from the week ending September 12, 1921, to the week ending March 28, 1922. The evaporation data, therefore, relate to most of the spring, all of the summer, and to one of the autumn months.

A summary of the evaporation-precipitation ratios for the period of the observations is given in table 10.

The Matjesfontein record, although short, is of interest because it suggests the extremely variable P/E values obtaining in an arid region. There was little or no precipitation in September, October, November, and February 1921-22, but 2.75 inches occurred December 25-28. Assuming, for purposes of comparison, that the non-effective amount for November occurred in October and February as well, we obtain extremely low ratios for those months. The high evaporation-rate for December is associated with the want of rain during 24 days of the month, at the time of mounting summer temperature.

The annual course of the P/E for Matjesfontein will thus probably be found to exhibit an extremely wide range. The ratio, as above appears, is very low for summer, and with 63 per cent of the precipitation occurring in winter, it can be expected to be correspondingly high for that season.

TABLE 10.—*Normal and current precipitation-evaporation ratios at Matjesfontein, October 1921 to February 1922, with current and normal rainfall.*

	Evapora- tion.	Normal precipi- tation.	Normal P/E.	Current precipi- tation.	Current P/E.
	<i>c. c.</i>	<i>inch.</i>		<i>inches.</i>	
Oct.....	1,605	0.58	0.000360	^a 0.11	^a 0.000068
Nov.....	1,989	.60	.000310	.11	.000005
Dec.....	2,297	.19	.000082	2.75	.00119
Jan.....	1,635	.28	.000016	1.55	.00093
Feb.....	1,431	.69	.000480	^a .11	.000005

^a No rainfall is reported, and for comparative purposes 0.11 inch is assumed to have occurred, as in the following month.

BEAUFORT WEST.

At Beaufort West, altitude 2,792 feet above the sea, the atmometer record at hand runs from the week ending August 22 to the week ending December 5, 1921.¹ Up to November the atmometer was situated in a garden, somewhat sheltered from the wind, but exposed to the sun most of the day. In November and December, however, it was removed and placed on the roof of an outbuilding, where it was exposed to the wind as well as to the sun.

At Beaufort West the annual rainfall is 9.56 inches, of which about 34 per cent occurs in winter and 66 per cent in summer. From this it will be seen that the station is largely under the influence of the rains of the warm seasons, especially of summer.

¹ Since the above was written the atmometer records for Beaufort West, covering the period between January 5 and May 29, 1922, have been received. The total evaporation for February was 568 c. c. and for March 400 c. c. The rainfall for the two months was 0.46 and 1.56 inches, respectively. That for March was normal, but that for February was 0.80 inch below. The normal P/E for February is 0.0022 and the current for the month is 0.00089. The normal and current P/E for March is 0.0039.

During the period given above the atmometer was read daily and daily maximum and daily minimum temperatures of the air were recorded. In August a minimum of 31° F. was observed, which was the lowest for the period, and in November an absolute maximum of 102° F. was recorded. The greatest weekly variation in temperature occurred for the week ending October 16, when the maximum was 98° and the minimum 43°. The greatest daily variation was 44° F. which was noted on two occasions, November 23 and September 30. The daily variation in temperature was especially large during fair weather and clear skies; when, however, rain was reported, as, for instance, on November 9, it was small, the maximum being 65° and the minimum 54° F. All of these conditions, as will be seen below, directly affected the rate of evaporation.

The water-loss from the atmometer in September was 1,414 c. c. and in October 1,381 c. c. During these two months, as above remarked, the atmometer was situated in a garden, not irrigated at the time, and somewhat protected from the wind. In November, when it was placed on a roof, the evaporation was 1,350 c. c. The least weekly evaporation was 181 c. c. and the greatest was 615 c. c., both of which occurred during the month of September, the former for the week ending the 12th and the latter for the week ending the 19th. In November the extremes were 165 and 429 c. c. According to the data at hand, the greatest water-loss occurring in one day was on October 26-27, when an evaporation of 69 c. c. was recorded. On October 26 the maximum temperature was 96° and the minimum was 59°, and on the 27th the maximum was 87° and the minimum 60° F. The least daily evaporation, 10 c. c., was recorded on September 3. The range of temperature for the day was from 43° to 67° F.

During the last week of October and the second week of November the atmometer readings are of interest from the fact that in the first instance the weather was fair and the temperature high, with favorable conditions for a high rate of evaporation, as was experienced as above noted, and in the second instance, the week in November, there was some rain. The total evaporation for the last week in October was 351 c. c. and for the second week of November was 165.4 c. c. The daily extremes in the amount of water lost during the last week in October were 30 and 69 c. c. and during the second week in November with rain they were 14.5 and 37.1 c. c. The course of daily evaporation during this week decreased from 37.1 c. c. for Monday to 14.5 c. c. for Wednesday. There was a slight increase on Thursday and a drop on Friday, from which day the daily amount increased until the following week. Rain was recorded on 5 days. On Monday it was 0.01, on Tuesday it was 0.95, on Wednesday it was 0.26, on Thursday it was 0.86, and on Friday it was 0.08 inch. The day next succeeding the fall of 0.95 inch the lowest rate of evaporation

was obtained, and on the day next following the fall of 0.86 inch, the next lowest, 15 c. c., occurred. After the intermediate amount of rainfall for Thursday the daily evaporation mounted, until on Sunday it was 33.4 c. c. During the week the mean temperature decreased daily from 80° on Monday to 59.5° on Wednesday, the day following the heaviest rain, increasing slightly on Thursday, following a smaller rainfall of Wednesday, and decreasing Friday to 53.5°, following the heavy rain of the previous day, after which it gradually increased to 56° on Sunday. The daily variation in temperature and of rainfall is thus reflected in the readings of the atmometer.

In table 11 are given the normal and current rainfall for the months of September to November, together with the monthly evaporation and the P/E.

TABLE 11.—*Normal and current precipitation-evaporation ratios (P/E) at Beaufort West for September-November 1921, together with current and normal rainfall.*

	Evapora- tion.	Normal precipita- tion.	Normal P/E.	Current precipita- tion.	Current P/E.
	<i>c. c.</i>	<i>inches.</i>		<i>inches.</i>	
Sept.....	1,414	0.659	0.00046	0.26	0.000183
Oct.....	1,381	.660	.00047	0.08	.000056
Nov.....	1,350	.700	.00051	2.45	.001074

The normal P/E at Beaufort West for the months of spring, so far as is told by the record of 1921, is relatively low, but considerably higher than at Matjesfontein for the same months, as would be expected from the greater evaporation at the latter place and the somewhat smaller rainfall. The larger current ratio for November, equaling that for December at Matjesfontein, indicates that the summer ratios may be relatively high.¹ Whether the amplitude of the annual P/E ratio at Beaufort West is as great as that for the other station, may be doubted, but can not be safely predicted in the absence of more complete evaporation records.

SWAKOPMUND.

At Swakopmund the atmometer record at hand is from July 1 to November 11, 1921. The atmometer was situated on the roof of a house which was about 14 meters above the level of the sea. It was exposed to the wind and to the sun.

The mean annual rainfall at Swakopmund is 0.67 inch. No rain occurred during the period of observation above given. It seems probable that the rate of evaporation at Swakopmund, therefore, is

¹ The normal P/E for February at Beaufort West is 0.0022, but the current ratio for 1922 was 0.00089. See preceding footnote.

little affected by the rainfall. But, on the other hand, the ocean fog, which occurs frequently, especially in the warm seasons, carries much moisture. An additional climatic feature, in addition to temperature, which modifies the humidity of the air, is the east wind, which may be hot and therefore a drying wind. Thus the observer at Swakopmund, in commenting on the current weather conditions, often mentions the occurrence of the east wind, with the remark that it is warm or hot, and he also comments on the presence of fog. The latter apparently may occur for days together. The east wind appears to have been especially frequent in July and in August, and there was some fog in these months as well. The most pronounced occurrence of fog, however, appears to have been in October, especially in the earlier part of the month. In late October the notation was made that the weather was pleasant. There was an immediate relation, as will appear directly, between these features of the climate and the rate of evaporation as revealed by the record of the atmometer.

The total evaporation for July was 1,039 c. c., for September it was 613 c. c., and for October it was 619 c. c. The August record is not complete. The greatest daily evaporation was 85.5 c. c., which was the average of the evaporation for 4 days, and the least daily evaporation was 12 c. c., which was the average for 11 days. Although thus there is a great variation in the daily amount of evaporation at Swakopmund, it appears, so far as the records on hand are concerned, that for the portions of the seasons studied the usual daily evaporation ranges between 20 and 30 c. c. During July the amount of evaporation was relatively large. From July 9 to July 13, for example, it was 342 c. c. At this time there were warm days and an easterly wind. From August 27 to September 5 the total evaporation was 111 c. c. This was a period of foggy days. During the first 11 days of November the total evaporation was 278 c. c. In September and October, except the period just given, the daily evaporation was 21.8, 19.3, 21, 25.7, and 25.2 c. c. daily, to give the daily average for successive weeks. In every instance where the daily evaporation was high it was associated with an easterly wind, and in every instance when the evaporation was low, as in late July, early August, and early October, there were days of fog. The rainfall records for Swakopmund from 1913 to 1920 do not note any precipitation for the months of July, August, and September, but the mean for October, for this period, is 0.07 inch. From this it will appear that the precipitation-evaporation ratio is frequently exceedingly low. For October it was 0.00011.

PRETORIA AND IRENE.

The atmometer records for Pretoria and Irene include two series at each station. At Pretoria two atmometers were situated in the rockery, at the Division of Botany. At Irene, 9 miles distant, one

station was near the river and one on a kopje. The altitude of Pretoria is 4,471 feet and that of Irene 4,805 feet above the sea.

The atmometer records at hand for Pretoria are from the week ending September 10 to the week ending December 31, 1921. Of these one only will be referred to in this place. The least weekly amount of water evaporated for the period was for the week ending December 9; it was 95 c. c. Between September 24 and October 6 the amount of evaporation was 590 c. c., or approximately 350 c. c. per week. This was probably the highest weekly rate. The average daily evaporation for the time was about 50 c. c.

The total amount evaporated for the month of October was 1,129 c. c. and for November 717 c. c. The normal rainfall for October at Pretoria is 2.95 inches, and the amount for the month in 1921 was 2.77 inches. The normal and current P/E ratios are therefore 0.0026 and 0.0024. The normal November rainfall is 3.89 and the amount for the month in 1921 was 4.68 inches. The normal and current P/E ratios are therefore 0.0054 and 0.0065.

At Irene the records are from August 31 to the close of the year 1921. The record of the atmometer placed near the river is complete for September, October, and November. The least weekly evaporation for this station was for the week ending November 26—141 c. c. The highest rate was for the week ending September 25, when the evaporation was 327 c. c.

The total evaporation for September was 1,095 c. c., for October 983 c. c., and for November 493 c. c. The annual rainfall at Irene is nearly the same as at Pretoria, so that in the absence of immediately available rainfall data for this station it will be assumed to be quite as at Pretoria, both as regards the normal and the current amounts for the months considered. For September the normal precipitation at Pretoria is 0.38 inch. The normal P/E for September at the river station, Irene, is therefore 0.00034. The rainfall for September 1921 was 0.90 inch, making the current P/E 0.00082. The normal and current P/E for October is 0.0030 and 0.0028, respectively. For November the two ratios are 0.0078 and 0.0094.

The station on the kopje, Irene, had a minimum weekly evaporation of 122 c. c. for the week ending September 10, and a weekly maximum of 328 c. c. for the week ending October 16.

The total evaporation on the kopje for September was 965 c. c., for October 1,094 c. c., and for November 564 c. c. Employing the precipitation for Pretoria as before, the following normal and current ratios for the P/E are obtained: September, 0.00039 and 0.00093; October, 0.0026 and 0.0025; November, 0.0068 and 0.0082.

It will be seen that in September the P/E ratio for the station on the kopje had a somewhat higher September ratio than the other station, but that in October and November the opposite condition

obtained. The low ratios for September and the higher ratios in the two later months of spring point to the possibly normal seasonal march of the moisture relations.

TABLE 12.—*Normal and current precipitation-evaporation ratios (P/E) at Pretoria and two stations at Irene, September to November 1921.*

	Normal P/E.			Current P/E.		
	Pretoria.	Irene.		Pretoria.	Irene.	
		River.	Kopje.		River.	Kopje.
September.....		0.00034	0.00039		0.00082	0.00093
October.....	0.0026	.0030	.0026	0.0024	.0028	.0025
November.....	.0054	.0078	.0068	.0065	.0094	.0082

SUMMARY.

The results of the preliminary studies on evaporation, as revealed by readings of the atmometer, are at present too fragmentary for important deductions or generalizations. Certain features of interest, however, are suggested, which can be mentioned.

The precipitation-evaporation ratio is an index of the comparative aridity of a station which is of value for purposes of definition. This gives either the normal or the current index, accordingly as the normal or the current rainfall is employed. With the accumulation of evaporation data the use of the normal and current evaporation will enhance the value of the ratios.

At none of the stations are the records of sufficient length to give the course of the aridity index throughout the year. But at the National Botanic Gardens the record is sufficiently long to give some idea of the extremes to be expected in the region of winter rains. The highest index is in July, when 0.0403 was obtained, and the lowest, 0.0005, was in January-February. Thus the differences in aridity as between the winter and the summer seasons at the station are very great indeed. In regions having most of the rainfall in summer other relations would be expected. Thus, at Grahamstown, the July ratio was 0.00072 and the ratio for October was 0.0038. At Irene the index for September was 0.00034 (river station), and in November it was 0.078. At Pietermaritzburg the records are for the warm season only and the indices are accordingly fairly high, ranging from 0.0029 to 0.0049.

For the two stations in the Central Karroo, the records for Beaufort West are September-November, and at Matjesfontein they are from October 1921 to February 1922. At the former station about 66 per cent of the rainfall is in summer and at the latter station about 63

per cent is in winter. Although at both stations the values are extremely low, they, however, appear to reflect the annual distribution of rain as a prominent controlling factor. This is particularly the case at Matjesfontein. The October ratio for this place was 0.00036, while that for January was 0.000016.

The generalization can be tentatively made that stations in regions having winter rains are relatively more arid than stations in regions where the precipitation is in summer. Under such conditions difference in temperature at the time of the dry period is probably the most important factor aside from the fact of drought. The suggestion has some support from data derived from observations on evaporation from free water-surface. Graphs showing the P/E for Kimberley, Johannesburg, and Cape Town are given in figure 8. The mean monthly P/E ratios for the three stations in the order given are 0.26, 0.44, and 0.51. As compared to Cape Town, therefore, the coefficient of aridity of Kimberley is 1.9 and of Johannesburg is 1.15. The annual precipitation at Johannesburg is about 25 per cent more than at Cape Town, 87 per cent of which occurs in summer.

GENERAL FEATURES OF THE VEGETATION, ESPECIALLY OF THE MORE ARID PORTIONS OF SOUTHERN AFRICA.

A visitor to southern Africa is struck with the great variety of herbaceous plants and shrubs, and with the paucity or total lack of trees. The wild-flower market on Adderley Street, Cape Town, and all the country he sees in spring are illustrations of the first, and the environs of the city, where the flowers are most abundant, the mountains, and the plains generally, abundantly illustrate the second and third impressions. Indeed, so far as forests are concerned, the visitor is likely to see none at all, unless he makes special trips along the southern or eastern coastal belts, or to certain mountains or to the northern tropics. The next strong impression is likely to be that a very considerable portion of the country over which he travels either is semi-arid or arid, and that such characteristics of the vegetation as he hurriedly notes are largely determined by this feature of the climate, and a somewhat closer acquaintance is not likely to wholly change these impressions.

Hardly has the visitor gotten well away from Cape Town, either by motor-car or by train, and the familiar sight of Table Mountain with its fringe of pigmy forest and forest patches, when the open and sparsely inhabited hinterland is entered, with agricultural interests in the lowlands. Here there are at present but few native trees, but occasional patches of shrubs are left undisturbed, suggesting their prevalence in earlier times. These recall portions of California

and of the Mediterranean region, as the seaward slopes of the Atlas Mountains, and indeed they are referred to as Cape macchia.¹

As the distance from Cape Town becomes greater, a gradual change is noticed in the vegetation which appears to indicate a smaller rainfall. Low hills here and there are seen to carry few shrubs, but those are low, often cushion-form, apparently species of *Mesembryanthemum*. A mountain gorge (Hex River canyon) is entered and the stream followed to a high pass. On one side one sees species of *Aloe*, with fleshy leaves, very like species of *Agave* of America, and *Cotyledon* with short, stout stems, dwarf trees with fleshy stem and branches. On the opposite side of the gorge are plants characteristic of the Cape region. There shrubs and herbaceous plants are abundant.

Crossing the pass, the course is set in an easterly direction and the Central or Great Karroo is entered. It is not long before the passing vegetation becomes more scattering and gradually changed from that predominantly sclerophyll to that predominantly succulent. The succulents are fairly small. Trees are confined to the water-courses. If the season is late winter, or spring, the plains and kopjes are brilliant with the wealth of flowers with which the herbaceous plants and low shrubs, especially species of *Mesembryanthemum*, are covered, and the Karroo has become a garden whose like is doubtfully to be found elsewhere.

Thus far the visitor has been passing through a region in which the rains are chiefly in the cool seasons to one where the summer rains begin to be felt, and finally, as the train climbs the escarpment in the northeasterly side of the Central Karroo, the region dominated by the rains of summer is entered. Here the vegetation again suffers a noticeable change. The succulents characteristic of the Karroo, and indeed sclerophyllous shrubs as well, are less abundant or largely wanting. Grass becomes the leading characteristic of the vegetation, at least of the plains. The country is apparently not so arid as the Karroo of lower altitude, farther to the south.

Passing across the northern portion of the Upper Karroo, and especially into and through Greater Namaqualand, more arid conditions are again largely encountered. Grass becomes a less important characteristic of the vegetation, shrubs are low, and scattering sclerophylls and trees are apparently confined to the savannah forest westward of the mountains, or to the most prominent water-courses.

Across the semi-arid plain (bajada) west of the mountains of the Protectorate of Southwest Africa, grass is again an important feature of the vegetation, but in places terete-stemmed euphorbias dominate. As the main mountains are left behind, on the way to Swakopmund, the vegetation becomes increasingly sparse and the region increasingly arid, until within 50 miles, more or less, of the coast true desert con-

¹ A guide to botanical survey work: Mem. No. 4, Botanical Survey of South Africa, p. 59, 1922.

ditions are encountered. This is the Namib, one of the most arid regions known, with a rainfall on the coast of 1 inch or less annually. Seasonal changes make here relatively little difference in the general appearance of such a country, where shrubs are small and are confined to drainage channels, where trees are along the main streams only, and where the ground is for the most part quite bare. Nevertheless, plants are to be found here of great interest and uniqueness, as *Welwitschia* and *Acanthosicyos*, although neither can be seen from the railway coach.

Retracing his course to De Aar, the visitor is again impressed by the vast treeless plains, the southern extension of the Kalahari, with bunch-grass and shrubs, mainly on the kopjes. Trees are confined to the immediate vicinity of the rare water-courses, as the Orange River. Northward from De Aar the High Veld is crossed, a region of grassy plains, and kopjes with shrubs and trees along the drainage channels. In places, however, where the plains are better watered, there appears a sparse covering of sclerophylls. The Zoutpansberg mountains are passed through at length, and here appear for the first time tree-like euphorbias, with fairly small trunks but with heavy crowns. North of the mountains the Low Veld is entered, with the open forest of low trees and high shrubs, and with scattering baobab (*Adansonia digitata*), which is the largest or at least the most massive tree of southern Africa. The presence of occasional groups of palms (*Phoenix* sp.) and the cultivation of subtropical fruits (at Messina) point to the subtropical or tropical character of the northernmost portion of the Union.

The High Veld and the Low Veld, as pointed out above, are served by rains in summer. The winters are dry and may be fairly cold. These environic characteristics are reflected in the abundance of grass and the presence of deciduous perennials as a marked floral feature as opposed to the almost exclusive development of evergreen species in the extreme southwest.

Finally, the visitor is impressed on every side with the evident close relation between the character of the vegetation, including often the local distribution, and the general facts as to the amount, and seasonal distribution of the rainfall. And an important feature of the environmental complex is the fact of often long yearly periods of drought, which may be associated with seasons of high temperature, in which event the aridity is particularly intense.

To the Little Karroo via Mossel Bay and George and through the Outeniqua Mountains from the Cape Peninsula gives the visitor interesting glimpses of the south coast. The road leads through large plantations of trees, including the *Pinus insignis* of California, which have the appearance of being unusually vigorous and free from diseases. An open farming country, rolling, and not far from the shore at any time, is crossed, and here and there the way nears the coastal

range of mountains, where sclerophyllous shrubs and occasional leafy succulents are met, and in the washes a few native trees. At George, owing to the large rainfall, which is equally distributed month by month through the year, the countryside recalls portions of England, with green fields and trees and shrubs along the streets, and has little in common with southern Africa as the casual traveler sees it. The roads through the mountains to Oudshoorn give at first glimpses of sclerophylls and later, as the northern slopes of the mountains lead to the Little Karroo, succulents of numerous kinds, many of large size, are to be seen. Trees follow the water-courses, and there is much cultivation, including fields of alfalfa as food for ostriches, the raising of which is here an important industry.

BOTANICAL REGIONS OF SOUTHERN AFRICA.

Turning from such general considerations, some of the leading characteristics of the vegetation of the subcontinent may be presented somewhat more exactly. Thus the leading botanical provinces as recognized by the Botanical Survey of the Union are outlined in figure 7. They have been characterized by Pole Evans as follows:¹

“That part of Africa which lies South of latitude 22° falls naturally into two main botanical regions—the Cape Region and the South African region. The former is of comparatively small extent and occupies the angular strip of country in the southwest portion of the Province of Good Hope. The latter is of vast proportions and covers the rest of the country under review. The vegetation of the Cape region has a remarkable uniformity of character, while that of the South African region exhibits a great variety of types ranging from typical desert to tropical forest. The Cape region differs from the South African region in one important climatic factor. It experiences a winter rainfall, whereas summer rains fall over the greater part of the South African region. This difference in the seasonal distribution of the rainfall is mainly responsible for the marked dissimilarity of the vegetation of the two regions. So different are they in aspect and composition that they have little in common and might well belong to two widely separated countries.”

There is a striking resemblance between the general aspect of the flora of the Cape region and that of the Mediterranean region, as well as that of portions of California. Pigmy forests are the rule, and there is a great variety of bulbous and tuberous plants. Species characteristic of the Cape “macchia,” or chapparal, are apparently projected along favorable lines of migration into the other botanical regions, where there is more or less mingling in a transition zone, as along the borders of the Karroos.

It is the South African region, however, with which this study is mainly concerned. This may be divided, according to the author

¹ The main botanical regions of South Africa, in A guide to botanical work. Bot. Survey of South Africa, Mem. No. 4, 1922, p. 49.

quoted above, into the following botanical provinces: the Namaqualand Desert province; the Karroo province; the Kalahari park and bush province; and the South African steppe and forest province. The extent and situation of the four provinces are indicated in the figure.

The first three botanical provinces range from desert to semi-arid and include a great variety of plant forms, mainly, however, with marked xerophytic characters. Nevertheless, there are well-marked differences, as the following characterizations, taken from several sources, including publications of the Botanical Survey, will indicate.

In the Namaqualand province the "general aspect of the vegetation is that of widely separated xerophytic shrubs and bushes, with a fair proportion of succulent plants in the low-lying valleys and on the rocky outcrops. Grasses do not form a conspicuous feature of the vegetation, but they occur on the high plateaus and sandy plains, where their vegetative period is short and where they are always of a tufted habit." In this province are to be found, among other species, *Aloe dichotoma*, *Euphorbia virosa*, *E. dinteri*, *Sterculia gurichii*,

FIG. 7.—Main botanical regions, after Pole Evans. I. Karroo province with position and extent of Central or Great Karroo indicated in southern portion, with upper Karroo nor of the escarpment. II. Namaqualand desert province. III. Cape region. IV. Kalahari park and bush province. V. High veld, in western portion, steppe and forest province in mountains, and eastern grass veld and coast forest area to the east.

Cissus crameriana, and *Pachypodium giganteum* on the hills; *Parkinsonia africana*, *Acacia hebeclada*, *A. tenax*, *A. hereroensis*, *Boscia foetida*, *Rhigozum trichotomum*, *Catophractes alexandri*, *Sarcocaulon burmanni*, *S. rigidum*, and *Hoodia gordonii* on the plains; *Euphorbia gregaria* in the low-lying valleys, and along the dry river-beds *Acacia giraffæ*, *A. albida*, *Combretum primigenum*, *Euclea pseudebenum*, *Tamarix articulata*, and *Sisyndite spartea*, to quote from Pole Evans.¹

In the desertic Namib the same writer gives the following as among the more typical species: *Acanthosicyos horrida*, *Arthræua leubnitziae*, *Euphorbia branchiata*, *Mesembryanthemum marlothii*, *Welwitschia mirabilis*, and *Zygophyllum stapfii*.

The Karroo province is divided into the Upper Karroo, or plains, lying between 3,000 and 6,000 feet above the sea, and the Karroo, which has an altitude of 1,000 to 3,000 feet. Pole Evans states:

“[The] country generally, except after recent rains, has a semi-desert appearance. The vegetation is composed largely of xerophytic shrubs, shrublets, and succulents. Trees are almost entirely absent except along the river-beds. Some of the more typical plants are: *Galenia africana*, *Melianthus comosus*, *Salsola aphylla*, *Euphorbia mauritanica*, *Mesembryanthemum spinosum*, *Aitonia capensis*, *Sutherlandia frutescens*, *Lycium afrum*, *L. austrinum*, *Chrysocoma tenuifolia*, *Pentzia incana*, *Othonna pallens*, *Arctotis stæchandifolia*, and *Gnidia polycephala*.”

In the Upper Karroo small shrubs belonging to the Compositæ are the dominating type, but in the Karroo proper succulents, usually small, dominate. Among these are species of *Aloe*, *Cotyledon*, *Gasteria*, *Haworthia*, *Mesembryanthemum*, and *Pelargonium*.

The Kalahari park and bush province, according to the same author, occupies the vast tract of country which forms the central portion of South Africa. This province extends into the Tropics. The vegetation is composed of trees, scattered bush, and grass. Over the greater portion of the country the general aspect of the vegetation is park-like. Toward the east, where the rainfall is higher and more regular, the bush becomes denser and thicker. Thorn trees, mostly species of acacia, are the dominating feature of the bush. Among the widely distributed genera which occur in the province are *Acacia*, *Boscia*, *Dichrostachys*, *Grewia*, *Olea*, *Peltophorum*, *Rhus*, *Royena*, *Tarchonanthus*, and *Zizyphus*. In the northern, tropical portion there are among other species *Adansonia digitata*, *Copaifera mopane*, and *Sterculia* spp. Of these the striking baobab tree (*Adansonia*) has already been mentioned. (Plate 5.)

The South African steppe and forest province occupies a large portion of the eastern side of South Africa, according to Pole Evans. “In marked contrast to the areas already dealt with, this tract of country is well covered with grass; in fact, grass is dominant every-

¹ Bot. Sur. So. Africa, Mem. No. 4, 1922, p. 51.

where except where forest patches occur." The topography is extremely varied, ranging from the sea-strand to the most important mountains of South Africa, and beyond to the High Veld, or steppe, with characteristic savannah-forest and steppe vegetation, consisting of large numbers of species, many of which have tropical affinities. It is in the eastern savannah that the large species of *Euphorbia* are to be found. This province has features of great botanical interest, certain of which will be referred to in another place and connection. On the steppe the dominant grass is *Themeda triandra*. The trees of the Drakensberg forest are made up largely of *Podocarpus elongata*, *P. latifolia*, *Olea laurifolia*, *Celtis kraussiana*, *Curtisia faginea*, and *Xymalos monospora*. In the savannah east of the mountains are *Acacia karoo* and others of this genus, *Dichrostachys nutans*, *Ehretia hottentotica*, and *Zizyphus mucronata*. The chief succulents are *Euphorbia grandidens*, *E. cooperi*, *E. ingens*, *Aloe ferox*, *A. bainesii*, and *A. marlothii*. The coastal forest includes many trees most of which have tropical affinities, and among the genera are *Rhus*, *Albizzia*, *Millettia*, *Harpephyllum*, *Macaranga*, *Rauwolfia*, *Hyphæna*, *Phœnix*, and *Strelitzia*.

VEGETATION IN PORTIONS OF NAMIB DESERT
AND OF CENTRAL KARROO.

Although, as mentioned earlier, the writer had an opportunity to see something of the flora of the Cape region of the Little Karroo, as well as of the High Veld and Low Veld, and of the Eastern grass veld between Pietermaritzburg and the sea, most of his attention was given to two stations in the Central Karroo, with a short visit to Southwest Africa and the Namib. The following pages, therefore, have to do mainly with the Karroo and the Namib, the former at and about Beaufort West, Prince Albert Road, and Matjesfontein, and the latter at Swakopmund and the region east for about 50 km., including the habitat of *Welwitschia*.

At the stations mainly studied observations were made on the most striking perennials, and numerous tests were made on the transpiring power of several. Local distributional characteristics are summarized in connection with the brief discussion next to follow, in which some account is given of root characters. Salient anatomical and morphological features, with their possible significance, follow the last, and finally the results of the work on the transpiring power is presented.

The plates to be found at the end of the general study are designed to illustrate the character of the vegetation and of the habitat in a manner and to a degree not possible by other means.

THE NAMIB.

The Namib was crossed on the way from Windhoek to Swakopmund.

In the relatively short distance, about 100 miles, which separates the mountains of Southwest Africa from the coast, an increase in aridity is experienced from semi-arid at the base of the mountains to desert along the sea. There is a corresponding marked change in the vegetation.

In the vicinity of Usakas, altitude 2,865 feet above the level of the sea, are good-sized trees, largely species of *Acacia*, on the flats, with park-like openings where grass occurs. On the lower slopes of the hills are shrubs and grass. To the west of Usakas, and for about 50 miles, is the transition between the *Acacia* park forest and the Namib Desert.¹

Near Aukas, altitude 2,981 feet, grass is abundant and there are clumps of a terete-stemmed *Euphorbia* forming massive clumps from 2 to 3 meters high and possibly 5 meters in diameter. In places these are so abundant as to constitute bush formation. A few miles west of Aukas the line swings out from the hills and enters a wide plain on which the *Euphorbia* is especially abundant, appearing to be the only shrubby species. But there are scattering grasses.

¹ Some notes on a journey from Walfish Bay to Windhuk. H. H. W. Pearson. Bull. Misc. Information, No. 9, 1907, Roy Bot. Gard. Kew.

At Ebony, at a somewhat greater altitude, the rolling plains are well covered with grass. There are scattering and small sclerophyllous shrubs but no euphorbias. This condition persists for a few miles, when with continuous and rapid decrease in altitude the aridity quickly becomes more intense and the Namib Desert is reached.

The flora of the Namib, in the vicinity of Swakopmund, is more diverse than the extremely small rainfall of the region would lead one to suppose. The plains are, it is true, fairly devoid of vegetation, but there are shrubs and even trees of some size along the bed of the Swakop River. Pearson states:

“On the rocky sides and sandy floors of the lateral valleys of the Swakop and the Khan are found *Welwitschia*, *Commiphora*, . . . *Aristidæ*, and other grasses, with *Aloe dichotoma*, Linn. f., *Sarcostemma viminale* R. Br., a cacoid *Euphorbia* with stems 6 to 8 feet high and a *Hoodia* (? *H. Gordoni* Sweet) of similar habit. These and other Namib forms here meet and mingle with plants belonging to the entirely different flora which prevails in the beds of the main rivers and consists of species which are at home on higher levels to the north and east where these rivers take their rise. The dry sandy bed of the Swakop at Haikamchab (750 ft. alt.) supports a flora rich in individuals and fairly so in species, which includes among its more predominant forms *Acacia albida* Del., the ‘Ana’ tree; *A. giraffæ* Wild., the “Camelthorn,” perhaps the commonest tree in Damaraland; *Ficus demarensis* Engl.; *Euclea pseudebenus* E. Meyer; *Tamarix articulata* Vahl.; the Walfish Bay *Caroxylon*, here a shrub 15 feet high, with an undergrowth of the sand-binding thorny grass, *Eragrostis spinosa* Trin., which covers large areas of the river-bed almost to the exclusion of other plants of low habit; a *Tribulus* (? *T. erectus* Engl.) 1 to 3 ft. high, with handsome yellow flowers; a white-flowered *Heliotropium* (? *H. albiflorum* Engl.); and a white *Cleome*. The margins of the sandy bed are in some places fringed by a dense scrub of reeds.”

The foregoing description of the vegetation of the main river-beds and lateral valleys applies to a region about 25 miles east of Swakopmund. This region, as stated above, is one of the habitats of *Welwitschia mirabilis*. According to Pearson, the area where this rare species occurs is about 25 miles north and south and about 15 miles east and west, but, also according to Pearson,¹ the species occurs in a second locality about 400 miles to the north. The eastern limit of its distribution appears to coincide with eastern limit of the penetration of the ocean fog, and the altitude seems to be 300 meters more or less. Where I saw the species was in a shallow wash, possibly 250 meters wide, which slopes gradually to the Swakop River, about 2 miles to the north. It was on the edge of a plateau. To the south was a rim of somewhat higher ground from which other shallow and smaller drainage channels made their way. The ground was quite bare of vegetation, except in the channels, where was seen a straggling line of scattered small shrubs. Of these the most conspicuous at the

¹ Some observations on *Welwitschia mirabilis* Hooker. H. H. W. Pearson. Phil. Trans. Roy. Soc. Lond., Ser. B, vol. 198, p. 269, 1906.

time, June 28, was *Zygophyllum stapfi*, with its compact growth habit and dark-green round and fleshy leaves (plates 2c, 3c). There also was *Asclepias filiformis*, with its wand-like shoots, and *Bauhinia marlothii*, with fairly large leaves, and *Arthræua leubnitzia*, with rather fleshy stems (plate 3A, 3B). Five specimens of *Welwitschia* were seen widely separated on the plain (plates 1 and 2). Of these, two were about 2 meters from tip to tip and the balance were smaller. It will be seen from the figures that the habitat of the species is extremely arid, although the presence of any vegetation indicates a certain amount of available water. In fact, the moisture relations are possibly better than nearer the coast, owing in part to the higher elevation. The occurrence of perennials along the small drainage-channels on the plain and in the bed of the Swakop River near the habitat of *Welwitschia*, suggests the presence of subterranean water. The heavy ocean fog, also, which penetrates as far as this place, probably aids directly as well as indirectly to alleviate the conditions of aridity. That *Welwitschia*, as well as *Bauhinia*, growing near by are in position to obtain water is evidenced by the fact that they give off water in transpiration, as mentioned in another place. In fact, the transpiring power of both of these plants on June 28 was found to be relatively high, which suggested that the species may not be so markedly xerophytic as the appearance of the habitat would appear to require.

Between the habitat of *Welwitschia* and Swakopmund the wagon-road goes for the most of the way on the south side of the river, but crosses it before reaching that town. The vegetation on the plateau and along the track is as just sketched. Here, in shallow drainage depressions, were seen *Arthræua leubnitzia*, with crowded fleshy branches, *Celosia spathulifolia*, *Senecio* sp., and *Zygophyllum stapfi*.

Crossing the river-bed some distance to the east of Swakopmund, one sees specimens of *Acanthosycios horrida* (plate 1), which forms clumps about which the sand congregates, forming hillocks. The species is leafless, but richly branched, and bears countless short, stout spines which are the homologues, according to Pearson, of tendrils. It is more xerophytic in appearance than in reality. It has long roots which tap perennial water-supply, and Pearson states that watery fluid exudes in drops from the cut ends of the assimilating stems. Although I searched several shrubs, I found but one fruit. The melons of this, the naras, are in great demand among the native blacks and constitute an important article of food, being eaten fresh in summer and dried for subsequent use in winter.¹

¹ The Namib was visited by the writer in June-July, 1921, when the fairly abundant flora of the Swakop Valley was seen. In March 1923, according to a correspondent, and as a result of unusually heavy rains in the mountains, the valley of the river was flooded, with the effect that "there is no trace of vegetation left in its bed, nor any tree on its banks for miles." From this it would appear possible that the "naras" may have been washed into the sea.

Species of *Tamarix* and *Nicotiana*, as well as of halophytic grasses, are common in the river-bed at Swakopmund, and the first named occurs occasionally among the sand dunes which lie along the south side of the river. On the plain back of the village there appears to be little or no vegetation of any kind.

THE CENTRAL KARROO.

BEAUFORT WEST.

At Beaufort West, in the northeasterly part of the Central Karroo, the vegetation of the dolorite kopjes near town was examined and some visits were paid to the wide mouth of a canyon about 6 miles east. The kopjes run in general northwest-southeast direction, so that there are northern and southern aspects.

In general it can be said that the veld around the kopjes and the kopjes as well have a vegetation which is mainly composed of sclerophyllous shrubs and shrublets, which on the plain are scattering, and on the kopjes are more numerous on the southern than on the northern side, but nowhere form a thicket (plate 8).

Two quadrats, 10 by 10 meters in size, and situated on the northerly and southerly faces about 100 meters apart, were studied somewhat intensively. The results give a fair picture of the character of the vegetation of the kopje, as well as the reaction of the vegetation to the two different aspects.

In the quadrat on the south face, 76 perennials were counted, of which there were *Lycium* sp., *Carissa ferox*, *Grewia cana*, *Euphorbia mauritanica*, *Cotyledon wallichii*, and *Mesembryanthemum* sp. (plates 7A, 8C). One of the characteristics of the quadrat was the occurrence of several different species in a single aggregate. Thus, for example, plate 9 shows *Gasteria disticha* growing at the base of *Euphorbia mauritanica* and *Lycium*, and in plate 10 *Crassula quadrangularis* is shown at the base of *Lycium* sp.

In the quadrat on the northern exposure, 45 perennials were found, among which were *Euphorbia mauritanica*, *Pentzia virgata*, and *Asparagus striatus*. Thus perennials of whatever kind are less abundant on the northern slope, and also the composition is unlike on the two aspects. On the northern exposure occur *Aloe schlechteri* and *Euphorbia stellæspina*, neither of which are on the opposite slope (plate 8A, 8B). On the other hand, such species as *Cotyledon wallichii* and *Crassula quadrangularis* of the southern aspect are not to be found on the northern side. Thus aspect "preference" is clearly indicated.

An attempt was made to determine possible differences in the two aspects as regards the evaporation power of the air, but without satisfactory success, owing to the removing of one of the atmometers with reservoir by some unknown person. However, the following was learned: For the week ending August 22 the atmometer on the upper

northern slope lost 562 c. c. of water, and during the same week the atmometer in Beaufort West, about 1.5 miles distant, had a water-loss of 314 c. c. On the following week the one on the southern slope lost 356 c. c. while the one in town showed 271 c. c. of water evaporated. These results indicate a probable greater dryness of the air on the northern than on the southern slope of the kopje, as well as the greater dryness of the stations on the veld as compared to the one in town.

Among other noteworthy species which occur on the upper slopes of the kopje is *Gymnosporia buxifolia* (?) which has the distinction of possessing spines of unusual size (plate 7B, 7C). These are apparently dwarf branches, inasmuch as at certain stages in development they bear leaves. One spine was found which was 17 cm. in length.

The following species, in addition to several which were not known, were found on the kopje: *Aloe schlechteri*, *Aptosimum indivisum*, *Asparagus stipulaceus*, *A. striatus*, *Aster filifolius*, *Carissa ferox*, *Cotyledon decussata*, *C. wallichii*, *Crassula quadrangularis*, *Euphorbia mauritanica*, *E. stellæspina*, *Gasteria disticha*, *Gazania pinnata*, *Gnaphalium* sp., *Grewia cana*, *Gymnosporia buxifolia* (?), *Hermannia spinosa*, *Indigofera* sp., *Kleinia articulata*, *K. radicans*, *Lycium* sp., *Massonia latifolia*, *Mesembryanthemum densum*, *M. spinosum*, *Nemesia* sp., *Osteospermum* sp., *Pentzia virgata*, *Royena pallens*, *Senecio longifolius*, *Stapelia* sp., *Ursinia* sp., and *Viscum rotundifolium* on *Gymnosporium buxifolium*.

The dolorite kopjes of which the vegetation was sketched in the preceeding paragraphs run nearly at right angles to Nieuweveld Mountains, immediately on the north, which separate this portion of the Central Karroo from the higher Upper Karroo. There does not appear at this place to be direct connection between the mountains and the kopjes along which plants of the two divisions of the Karroo can readily migrate. Accordingly advantage was taken of visiting the mouth of a canyon opening toward the southwest from the Nieuweveld Range and distant from Beaufort West about 6 miles. The mouth of the canyon is flanked on either side by flat-topped projections from the main range. There are long talus slopes ending abruptly at pronounced cliffs. From the stream to the mesas above is possibly a vertical distance of 1,000 feet. Although the kopjes nearer Beaufort West are overrun by sheep and goats, so that the vegetation at present to be found there are species of no economic importance, this is apparently not so much the case at the canyon referred to. Even here, however, there are not only wandering flocks, but a natural fauna that in part lives on its vegetation. There are, for example, among the less accessible cliffs various "bocks," baboons, etc., which range through the canyon and go to the canyon floor near its mouth for water.

The floor of the canyon, as well as the sides, are well covered with vegetation, which, however, appears to be more abundant on the south (?) side than on the north side and most abundant on the floor.

The number of trees and shrubs in the canyon is apparently considerable. By the water is the arboreal species *Rhus lancea*, willow-like in appearance, and *Lycium* sp., and near the stream are *Gymnosporia buxifolia*, *Mesembryanthemum unidens*, *Senecio longifolius* (plate 13), *Sutherlandia frutescens*, and others.

On the south (?) side of the canyon the woody perennials are mainly about 1 meter in height and largely, if not exclusively, sclerophylls. There are no trees. Among the species seen are the following: *Buphane distacha*, *Cussonia spicata*, *Cadaba juncea*, *Cotyledon decussata*, *Crassula perfossa*, *Eriocephalus* sp., *Euclea undulata*, *Grewia* sp., *Hermannia canescens*, *Lobostemon* sp., *Othonna pavonia*, *Pachypodium bispinosum*, *Pelargonium tatragonum*, *Pteronia incana*, *Rhus* sp., *Senecio cotyledonis*, *S. longifolius*, *Stachys* sp., and *Thesium* sp.

Of these species, *Cussonia* occurs only at the immediate base of the escarpment and in few numbers, and the balance are apparently less restricted, both as to distribution and abundance.

On the opposite side of the canyon there appears to be a much larger proportion of succulents, especially of the leaf-succulent type, and, as before mentioned, the vegetation does not seem to be so abundant. Among other species occurring on this side are the following: *Bulbine rostrata*, *Cotyledon orbiculata*, *Crassula perfossa*, *Mesembryanthemum angulatum*, *M. haworthii*, *M. nobile*, and *Pachypodium*.

Many of the genera to be found in the vicinity of Beaufort West also occur in the Upper Karroo, where the Compositæ appear to be especially well represented. On the other hand, as will be seen from the short species lists given above, there are many succulents as well as sclerophylls in this region, by the former of which it establishes its Karroid nature. The flora of the immediate region may possibly be intermediate, therefore, between that of the Central and of the Upper Karroo.

PRINCE ALBERT ROAD.

Prince Albert Road, altitude 2,012 feet, is 74 miles southwest of Beaufort West and lies fairly in the central part of the Central Karroo. The rainfall, average of 25 years, is 4.57 inches annually, with a minimum of 3.34 inches. It therefore is one of the most arid stations of the Karroo.

Prince Albert Road is situated on a plain which extends in a southerly direction 25 miles, more or less, to the Groote Zwarte mountains, but which on the north meets the foothills of the Nieuweveld Mountains at no great distance. Excursions were made to the low hills about 2 miles from town.

On the flats by the village *Hibiscus urens* occurs. The species has the habit of a cucurbit, for which it could be easily taken. Marloth makes the statement that the leaves are thickly covered with trichomes, that the species succeeds in the most arid situations, and comes into flower in the middle of summer.¹ The plant is remarkable from the fact, among other features, that the leaves are actually large and the total leaf-surface of the plant extensive, which would hardly be expected in so arid a habitat.

Beyond the *Hibiscus* habitat the plain insensibly merges into a poorly defined wash, beyond which are narrow and flat-topped hills, which in turn retreat to the mountainous background, leaving narrow and long valleys between. In and along the wash are *Acacia karroo*, leafless in June–August, *Carissa ferox*, and *Tamarix* sp. There also are various species of grass.

Beyond the wash are low and small rounded hillocks on which are scattering cushion-like and small succulents, *Mesembryanthemum calamiforme* and *Cotyledon hemisphærica* (?), with bare ground between (plate 11). In a quadrat 10 by 10 meters, 175 individuals, mainly of these two species, were counted.

The vegetation of the long hills and valleys is varied and fairly abundant, and includes among others the following species:

Aster sp.	Lycium sp.	M. uncinatum.
Berkheya obovata.	Mesembryanthemum ana-	M. uniflorum.
Cotyledon decussata.	tomicum.	M. viride.
C. hemisphærica.	M. brevifolium.	Monechma sp.
C. wallichii.	M. calamiforme.	Pteronia sp.
Crassula lycopodioides.	M. croceum.	Rhus sp.
C. perfossa.	M. crystallinum.	Royena pallena.
C. tetragona.	M. floribundum.	Sarcocaulon sp.
Dicoma diacanthoides (?).	M. haworthii.	Sutherlandia frutescens.
Galenia africana.	M. junceum.	Tetragonia sp.
Geruleum bipinnatum.	M. magnipunctatum.	Tripteris sinuata.
Geigeria passerinoides.	M. spinosum.	
Hermannia sp.	M. splendens.	

There are in addition numerous other species, including grasses, although the latter are not abundant.

It will be seen that succulents are prominently represented at Prince Albert Road. This is especially true of the slopes and hills.

MATJESFONTEIN.

Metjesfontein, altitude 2,955 feet, has a rainfall of 6.88 inches annually, and although thus the precipitation is no greater than at many Karroo stations farther east, the vegetation, immediately about the town at least, is probably not to be considered typically karroid. The situation of the station is in the extreme westerly edge of the Central Karroo.

¹ Das Kapland, l. c., p. 220.

The typography is various. The Wittebergen are to the south, and a western continuation of the Nieuweveld Range is to the north. The former is possibly 5 miles distant and the outliers of the latter not over 2 miles away. Between is in effect a wide valley which on the east descends fairly rapidly to Laingsburg, 2,167 feet altitude, 18 miles distant, and on the west ascends rapidly to Pietermeintjes, distant 10 miles, altitude 3,585 feet. At Laingsburg the annual rainfall is 4.62 inches, while at Pietermeintjes it is 13.8 inches. Although the annual rainfall at Matjesfontein is relatively small, the topography of the vicinity and its relation to the highlands both to the north and to the south, as well as to the higher valley west, make it altogether possible that the valley vegetation at least is largely determined by the telluric waters.

The vegetation at and in the neighborhood of Matjesfontein is exceedingly varied, the species are many, and the plant population as a rule large. Both sclerophylls and succulents are well represented and there are numerous bulbous species. Only a brief account can be given here of the vegetation, mainly for the purpose of forming a background for the discussion of studies on the transpiration of a few species which were carried on at Matjesfontein, Whitehill, and Tweedside.

The leading physiographic formations in the immediate neighborhood of Matjesfontein appear to be (1) stream-way, (2) plain or valley floor, (3) rocky outcrops, (4) kopjes, and (5) kopje slopes. Of these, it need only be said that the kopjes visited were from about 100 to about 1,000 feet above the surrounding plain. By rocky outcrops is meant areas on the plain, often of relatively small extent, on the surface of which are stones, sometimes apparently in place, which rise a few feet only above the plain, or such as occur along the stream-ways. This formation is not sharply marked, however, although it is probably of considerable extent when taken altogether.

The vegetation along the main stream is characterized by *Rhus viminalis*, *Acacia karroo*, and *Lycium* sp., of which the species of *Rhus* is confined to the banks, while the other species may wander over the flood-plain or bottoms adjacent.

Some quadrats were made on the valley floor and on areas where there was outcropping of rocks. These give sufficiently well for the purpose at hand the nature of the vegetation of such formations.

An area 10 by 10 meters in size, situated about 0.75 mile west of the village of Matjesfontein and well in the valley, was studied. The soil was somewhat sandy and there were no stones on the surface. The vegetation consisted of sclerophylls, with some bunch-grass and many small flowering species, bulbous and otherwise. In this quadrat 49 individuals, sclerophylls, were enumerated. The dominant species was *Galenia africana*, with a few *Chrysocoma tenuifolia*, *Pentzia virgata*,

and *Lycium* sp. There were no succulents. The individuals were large and the ground was well covered by them.

Quadrat No. 2 was on the lower slope of a kopje not far above the quadrat just characterized. It was well out of the valley floor, there were scattering stones about, and the soil was fairly coarse. In this quadrat 345 individuals were counted, all of which were small sclerophylls. *Chrysocoma tenuifolia* was the dominating species, although there were many of *Pentzia virgata* as well. Succulents were wanting. There were few small flowering plants and few grasses. The soil between the shrubs was mainly bare.

The third quadrat (plate 12A) was on a low, rocky outcrop, situated about a mile east of the village and in the midst of the valley. The soil was fairly coarse and there were stones of various sizes, some possibly in place, which appeared on the surface. There were counted in a representative area 10 by 10 meters, 330 individuals, of which 160 were sclerophylls and 170 were succulents. All of these were small, in part probably from the effects of grazing. The following species were found: *Aster filifolius*, *Cotyledon orbiculata*, *C. reticulata*, *Crassula columnaris*, *Eriocephalus* sp., *Helichrysum ericifolium*, *Pelargonium* sp., *Pteronia glomerata*, *Stæbe* sp., and *Tetragonia* sp.

Another quadrat, No. 4 (plate 21), where there also were rocks strewn on the surface, and possibly some in place, was studied about 1.5 miles to the north of Matjesfontein. This was a slope not far from a kopje, although it appeared to be quite independent of the latter. Here 397 individuals were counted in an area of the same size as before, of which 213 were succulents. *Mesembryanthemum spinosum* dominated, but of the sclerophylls *Pentzia virgata* was most numerous. There was hardly a sclerophyll but what had one or more small succulents beneath. Among the succulents were two species of *Mesembryanthemum* with cushion-like habit, *Crassula columnaris*, and others. *Asparagus capensis* was often associated with *Pentzia virgata*.

In quadrat No. 5, which was on the plain, there were large sclerophylls. Here were *Chrysocoma tenuifolia*, *Elytropappus rhinocerotis*, *Galenia africana*, and *Mesembryanthemum spinosum*. *Mesembryanthemum* dominated.

Different species dominate in different portions of the veld by Matjesfontein, as has already been mentioned. Although this may be seen in several places, it was especially noted in an area to the south of but not distant from the village; the water conditions were apparently especially favorable, as the plain was a bajada coming from the hills to the south. At the place referred to *Elytropappus rhinocerotis* either dominates or in places constitutes the only species. The plants are often 1.5 meters high. A feature of the *Elytropappus* habitat is the lack of smaller plants clustered about the base of the

larger and dominant species, growing under their "protection," as is so commonly the case in the Karroos.

The flora of the kopjes is especially rich both as to numbers and species. Here, among other species, occur *Aloe striata* (?), *Cotyledon coruscans*, *C. orbiculata*, *C. paniculata*, *Crassula perfossa* (plate 16), *Euclea undulata*, *Euphorbia mauritanica* (plate 17), *Lebeckia psiloloba* (plate 20), *Mesembryanthemum junceum* (plate 15), *Mesembryanthemum* sp., and *Rhus* sp.

In limited areas in the immediate neighborhood of Matjesfontein, but over large areas in the valley about 8 miles north, there occur *Mesembryanthemum* sp. in cushion-like habit, almost to the exclusion of other species. At Majesfontein there are rarely, if at all, monospecific communities, although in certain instances, as that just given, certain growth-forms may be the rule. Over limited areas also a single species may constitute 80 per cent of the entire population, as, for example, about 1.5 miles north of town, where on a gentle slope *Mesembryanthemum spinosum* dominates. The shoot of this species is much branched, and the small, fleshy leaves are numerous, so that the ground beneath is well shaded. Possibly for this reason, although the shallow placing of the roots may be contributory, the species usually occurs singly. When *Galenia africana* is associated with it, the latter is often small, but when it is with *Elytropappus rhinocerotis* both appear equally vigorous. In the case of *Galenia*, as will be mentioned elsewhere, it is possible that the transpiring power is especially large and that an abundant water-supply is essential, which might not be possible to obtain were the species closely associated with *M. spinosum*.

There are many species at and in the vicinity of Matjesfontein, some of which are scattered here and there about the valley, while others are of even more restricted distribution. Of such species the following, some of which are illustrated in plates 13 to 31, may be mentioned:

<i>Aloe variegata</i> .	<i>E. multiceps</i> .	<i>P. crithmifolium</i> .
<i>Anacampseros papyracea</i> .	<i>E. stolonifera</i> .	<i>Pentzia virgata</i> .
<i>Buphane disticha</i> .	<i>Euryops lateriflorus</i> .	<i>Protea neriifolia</i> .
<i>Cotyledon mamillaris</i> .	<i>E. tenuissimus</i> .	<i>Pteronia flexicaulis</i> .
<i>C. orbiculata</i> .	<i>Haworthia margaritifera</i> (?).	<i>P. glomerata</i> .
<i>C. paniculata</i> .	<i>Hyobanche glabrata</i> .	<i>P. incana</i> .
<i>C. reticulata</i> .	<i>Lebeckia psiloloba</i> .	<i>P. pallens</i> .
<i>C. wallichii</i> .	<i>Loranthus glaucus</i> .	<i>Relhania squarrosa</i> .
<i>Crassula columnaris</i> .	<i>Mesembryanthemum crys-</i>	<i>Rhus viminalis</i> .
<i>C. lycopodioides</i> .	<i>tallinum</i> .	<i>Stapelia pillansii</i> .
<i>C. perfossa</i> .	<i>M. junceum</i> .	<i>Sutera cœrulea</i> .
<i>C. portulacea</i> .	<i>M. pygmæum</i> .	<i>Sutherlandia frutescens</i> .
<i>C. tetragona</i> .	<i>M. spinosum</i> .	<i>Thesium horridum</i> .
<i>Euclea undulata</i> .	<i>M. quadrifidum</i> .	<i>T. spinosum</i> .
<i>Euphorbia hystrix</i> (?).	<i>Pelargonium alternans</i> .	

NOTES ON ROOT HABITS.

Some notes were made on the root habits of several perennials which occur naturally at and in the vicinity of Matjesfontein. The species studied were both sclerophylls and succulents. The habitats were mainly the plain and along the stream-way. The following is a brief statement of the leading results.

Cotyledon coruscans (plate 24B, 24c) was observed on the veld, plain, near the village. The root system is poorly developed and superficial. In the specimen studied the main root forked near the crown, but there were relatively few rootlets.

The specimens of *Cotyledon reticulata* examined were growing near *C. coruscans*. This succulent is about 15 cm. high and has branches 5 cm., more or less, in diameter. There is apparently no tap-root, but several roots of equal rank arise from the base of the stem. They take a horizontal course, keeping always near the surface of the ground. The roots branch frequently and there are numerous filamentous rootlets.

The specimen of *Cotyledon wallichii* (plates 16 and 18) examined occurred on the veld where stones were scattered on the surface. The soil was fairly deep, however, and much exceeded the depth to which the roots penetrated. The specimen was mature, the shoot being about 35 cm. high. There were two kinds of roots, of which one sort reached as far as 82 cm. from the base of the stem. This was composed of five roots, each of which was about 1.8 cm. in diameter at the base. The extreme depth attained by them was 7.5 cm. The second type of roots were short and numerous, and arose from the root crown. They bore groups of filamentous roots which had the appearance of being short-lived.

Crassula lycopodioides (plate 30B) has a meager root-system. The roots are few and all superficial. None were found over 10 cm. deep, and for the most part they were within 5 cm. of the surface.

Elytropappus rhinocerotis is fairly abundant on the plain at Matjesfontein and becomes increasingly so as one goes west, where the rainfall is greater. The root-system of the species was not especially studied, although observations were made in certain instances. There is a well-marked development of superficial roots (plate 27); some of these are large and give rise to shoots, as in the case of *Lycium* sp.

Euphorbia multiceps (plate 25A, 25B) occurs at Matjesfontein on the valley floor and the specimens examined were situated where the soil was relatively deep. The main root is especially well developed and in the specimens examined appeared to strike deeply and did not send out superficial horizontal roots. Where the main root was forked the two branches continued to go downward. This an unusual type of root-system for a succulent.

An undetermined *Euphorbia* with growth habit much like *E. mauritanica* and which was growing in a rocky place on the veld had a short and succulent or at least stocky tap-root which penetrated the soil 10 cm. and then branched, and the latter continued downward. There appeared to be no superficially placed horizontal roots.

Euryops lateriflorus occurs at Matjesfontein in a rocky outcrop by the stream near the village, where the transpiration studies on the species were carried out, but the roots were examined at a place 7 miles west, where the soil is deeper and the rainfall greater (plate 23). In the immediate vicinity of the plants examined were found *Elytropappus rhinocerotis* and other sclerophyllous shrubs, in addition to *Euryops*.

The specimens were growing on the edge of a shallow "box" canyon and the roots had been partly exposed by erosion. The root system is characterized by a pronounced tap-root and quite as pronounced laterals which are horizontally placed. The tap-root was over 40 cm. long. The laterals arose about 5 cm. beneath the surface of the ground and extended for a distance of 32 cm., more or less, maintaining about the same depth throughout their course. Another specimen had the same character of roots, but the main root was found to penetrate somewhat more deeply.

Galenia africana is very abundant on the flats by the stream at Matjesfontein. Where the roots were examined the banks were from 2 to 4 meters above the water itself and the soil had been eroded, leaving perpendicular walls. Plate 22 illustrates the character of the roots of the species. There is a well-defined main root which may attain to a depth of 3 meters or more. The secondary and tertiary roots are numerous. Important branches go fairly directly downward. Many small roots arise at the crown of the main root and extend outward horizontally for 1 meter, more or less. They are essentially superficial. At a depth of about 50 cm. other laterals arise and take a fairly horizontal direction in growth. Deeper than this the laterals are not so numerous, and they appear to assume a more nearly vertical position than those more superficially placed. The root-system of the species, therefore, is especially well developed. It penetrates deeply and reaches out widely.

In *Galenia* each plant appears to arise *de novo* and not from underground organs of any kind.

The specimens of *Lycium* sp. (plate 27) whose root-systems were examined were growing in the vicinity of *Galenia africana* last described and under the same soil conditions. The species has a pronounced tap-root which penetrates the ground 2 meters or more. The main root does not branch freely. At a depth of about 50 cm. several large laterals arise and go nearly directly downward. There are few relatively small laterals near the crown of the main root, and one or more

prominent laterals 30 cm., more or less, beneath the surface. Immediately below the surface of the ground were one or more large superficial roots which gave rise on the one hand to numerous roots which went directly downward, and on the other hand to branches. Vegetative reproduction appears to be a well-established method of propagation in this species.

Mesembryanthemum junceum (plate 26) is a much-branched shrub bearing small fleshy leaves and occurs on the plain in the vicinity of Matjesfontein, often in association with *Galenia africana*. The roots appear to be mainly superficial. In one specimen which was examined 13 laterals arose about 6 cm. beneath the surface and extended outward, maintaining fairly closely this depth, and another but somewhat smaller plant of the same species, having a shoot 15 cm. high, had a well-marked main root which, tapering rapidly, forked at a depth of 12 cm. Several laterals arose near the surface of the soil and extended in a horizontal direction for a distance of 30 cm. or more.

Mesembryanthemum spinosum (plate 26) also occurs on the plain and appears to have a root-system resembling that of the species last described, in that it is mainly superficial. There is a main root which does not appear to penetrate deeply. Numerous laterals are given off near the surface, which in one instance were found to extend to the base of the neighboring plants, *Cotyledon wallichii* and *Galenia africana*, about 1.25 meters distant. As regards both species, it is possible that under appropriate conditions of soil and of soil moisture deep root penetration might take place.

In *Pelargonium crithmifolium* (plate 31B) which occurs on low and somewhat stony hills near the village, there is a stout and short stem and a much-enlarged root crown with well-defined main root. There do not appear to be many laterals, and none which lie close to the surface of the soil. The root-system can be characterized as being poorly developed and meager.

Other species of *Pelargonium* of similar growth habit in the same vicinity had the character of root as just briefly described. In one specimen where the root crown measured 2.5 by 5 cm. in cross-section, the main root was traced into the stony soil to a depth exceeding 18 cm., during which distance no laterals were given off. The depth attained by the root was not learned. However, it appears probable that in the vicinity of Matjesfontein the roots of species of *Pelargonium* of this type do not have superficial roots, but that on the contrary they are fairly deeply placed. A similar condition was noted also in *Euphorbia multiceps*. Both of these species with water-storage capacity thus constitute an apparent exception to the frequently observed root habit of succulents.

Salsola aphylla was observed on the flats back of the Karroo Botanical Gardens, Whitehill, where the roots had been exposed along a

narrow wash by erosion. The root system was characterized by a well-developed tap-root whose depth exceeded 45 cm. The few laterals were, for the most part, about 5 cm. beneath the surface of the ground. They extended 26 cm. or more away from the main root. In one instance such a lateral was seen to turn and run directly downward 45 cm.

Stapelia pillansii (plate 28D), which occurs on a small rocky outcrop about 0.5 mile east of Matjesfontein, has short and much-branched roots, all of which appear to be shallowly placed. They extend from the plant cluster only a few centimeters. The root-system, therefore, is poorly developed.

Rhus viminalis (plate 20) is confined to the immediate vicinity of the stream at Matjesfontein. It therefore occasionally happens that the roots are exposed through the washing away of the banks. About a mile east of Matjesfontein there has been marked and recent erosion along the stream-way. In one instance several roots of *Rhus* were laid bare. In this case there appears to have been a marked root development at, or not far above, the water-level. For example, one root was traced more than 25 meters, and for most of the way it lay about 1.5 to 2 meters beneath the surface of the stream-bank. There was a well-developed main root, the depth of the penetration of which, however, was not learned.

From the failure to find species with succulent roots, other than certain bulbous forms, it is not to be concluded, however, that such are wanting in the vicinity of Matjesfontein or of Beaufort West, where most of the studies on the plants in the field were carried out. Thus *Pachypodium bispinosum*, which was found growing on the side of a gorge 6 miles east of the latter place, but which was not especially examined, is known to have tuberous roots. Marloth¹ figures the enlarged roots of this species as well as those of other species. An apparent exception to the first statement is to be found in *Haworthia* sp. (plate 29A), in which, as will be seen, the shallowly placed and radiating roots are somewhat tuberous. In this species the shoot is not succulent, so that a succulent condition of the roots may be a specific quality. Succulency, both of root and of shoot in the same species, does not seem to occur. It can be concluded, therefore, that root succulency is not common at Matjesfontein and probably not at Beaufort West.

SUMMARY.

It will be seen, therefore, that the roots of the plants examined can be conveniently grouped into those with a well-developed main root, as in *Euphorbia multiceps* and *Pelargonium crithmifolium*; those with both main root and laterals both well developed, as in *Elytropappus*,

¹ Das Kapland, l. c., p. 316.

Euryops, *Galenia*, *Lycium*, *Salsola*, and *Rhus viminalis*; and those with superficial roots, as in *Cotyledon*, *Crassula*, certain species of *Mesembryanthemum*, and *Stapelia*.

Euphorbia multiceps and *Pelargonium crithmifolium* are succulents and as such would be expected to have poorly defined main root, with laterals originating near the surface of the ground, or with roots of equal rank, but in any event with roots which do not penetrate deeply. In such position advantage is taken of very light rains. In the case of these species, however, so far as the observations extended, it appeared that even when the downward progress of the main root is turned, or stopped by rocks, the type of the root nevertheless does not become changed. The prominent development of the main root in the two species appears, therefore, to be obligate.

The balance of species with succulent habit, either of stem, leaf, or root, have as a rule a meager root-system. In some species the roots reach out but a few centimeters from the base of the plant, but in others they extend so far as 82 or 125 cm. In any event, they lie within a few centimeters of the surface.

The sclerophyllous species all appear to have roots which vary to a certain and possibly usually considerable degree as regards the depth and lateral extent of development, but they all agree on having relatively large development of the root-system. In *Elytropappus rhinocerotis* the superficial roots are a prominent feature, and in *Galenia africana* there are many small roots about the base of the stem, but in both species there are also deeply penetrating roots. Observations indicate that *Elytropappus* may occur to the exclusion of other species, especially small succulents which often are found gathered about the base of sclerophylls. The presence of numerous superficial roots in the species may be a contributing factor to this condition. That there may in fact be some sort of distributional adjustment between species on the basis of difference in root types, or possibilities in the direction of development, seems not unlikely. Thus there is often an association of shallowly rooted and of deeply rooted species, as mentioned above. Where species requiring a good supply of water, such as the sclerophylls in question, are closely associated, the effects of the subterranean competition may be evident from the poor shoot-growth on the part of either, or both. Thus it was noted that when *Galenia africana* was associated with *Mesembryanthemum spinosum*, the shoot of the former is often small, but when *Elytropappus* occurs in association with the *Mesembryanthemum* the shoot development of the species (*Elytropappus*) is apparently quite normal. As all of these species have different types of generalized roots, there is possibly some sort of mutual adjustment and accommodation in the last-named instance, which is lacking in the one first referred to, and this may well be in connection with the roots.

In *Lycium* sp. and *Elytropappus rhinocerotis* shoots arise from stolon-like roots, which is probably to be considered an important way of winning territory and of holding that already occupied, as well as of repelling invading species.

SOME FEATURES OF FOLIAR STRUCTURE.

The results of studies on the inner morphology of the perennials of foreign regions, particularly of central Australia, led the writer to examine that of some of the plants observed by him in southern Africa. Not all of the plants studied in the field, however, were used, for the following reasons: In case of material which was collected and immediately placed in suitable reagents, or of living material, and there was a little of each, there was no difficulty, but where the material available was dried, as for the most part was the case, the matter was quite different. In the last event only species with a large amount of supporting tissue could be utilized, so that much of it—all in fact that was not available in the conditions first referred to—had to be discarded. These facts are of interest for the reason, as will be referred to later, that under arid conditions the relative amount of cell-wall stuff organized by the plant may be very large, but under less arid conditions the type of metabolism is quite different, possibly leading to the ultimate formation of mucilages. Also, leaves of essentially mesophytic structure are not well suited in the dry form for such studies. These facts have worked to materially limit the scope of the structural studies. The studies are further limited by the fact that only leaves of winter were used, so that such forms as were in leaf in summer, as, for example, the acacias, could not be utilized.

The limitations in material have made it advisable to confine the treatment of structure to leaves, or at least to chlorophyll-bearing organs. Begun in the first place on species which were used in the studies on foliar transpiring power, the work was extended so that it finally included all material suitable for examination. This material, it should be remarked in passing, had been studied in various ways, other than that mentioned above, in the field.

Leaves of perennials of an arid region usually exhibit features which may not only be characteristic of the species, but of xerophytes in general. In spite of this, however, it is doubtful if any foliar structures of species of an arid region are really “new,” that is, quite characteristic of them and of no others. The differences are, perhaps, rather of quantity than of quality, although the quantitative differences may be great indeed. There need only be called to mind the formation of a heavy outer epidermal wall, or of much supporting tissue, or the frequent deep placing of stomata, or the formation of palisades, or the organization of mucilages, not to extend the list. But there is the background of heredity on which present-day forces play and which

makes the development in any given direction possible. This will be mentioned again later. But it is doubtless on account of such a conservative factor that there is the apparent limitation as to structure above referred to; and, finally, regarding organs which, like leaves, are directly affected by the environment, it is rather a matter of surprise that so much and not so little of possible ancestral qualities are to be found in them to-day.

An examination was made of the leaf structure of the following species:

<i>Aloe variegata</i> .	<i>Eriocephalus</i> sp.	<i>Pteronia incana</i> .
<i>Antizoma capensis</i> .	<i>Euclea undulata</i> .	<i>Relhania squarrosa</i> .
<i>Asclepias filiformis</i> (?).	<i>Euryops lateriflorus</i> .	<i>Royena pallens</i> .
<i>Asparagus striatus</i> .	<i>Galenia africana</i> .	<i>Rhus viminalis</i> .
<i>Bauhinia marlothii</i> .	<i>Grewia cana</i> .	<i>Rhus</i> sp.
<i>Cadaba juncea</i> .	<i>Gymnosporia buxifolia</i> .	<i>Stachys</i> sp.
<i>Carissa ferox</i> .	<i>Pentzia virgata</i> .	<i>Stoebe</i> sp.
<i>Cotyledon paniculata</i> .	<i>Protea neriifolia</i> .	<i>Sutherlandia frutescens</i> .
<i>Cussonia spicata</i> .	<i>Pteronia flexicaulis</i> .	

NOTES ON LEAF STRUCTURE.

ALOE VARIEGATA.

The material of *Aloe variegata* which was examined was living and had been collected in the vicinity of Matjesfontein.

Two leaves of the same plant were studied, of which one was older and smaller and was placed near the base of the rosette, and the other

FIG. 8.—*a*, Cross-section of leaf of *Aloe variegata* to show the heavy outer epidermal wall, with the cuticularized portion indicated by dotted lines, and the deeply placed stomata. $\times 300$.

b, *Asparagus striata*, cross-section of leaf, showing the heavy epidermis with thickened outer wall, the limited development of palisades, and a portion of a centrally situated mass of sclerenchymatous tissue. $\times 300$.

c, *Protea neriifolia*, section of an old leaf, in which is indicated the heavy epidermis with much thickened outer wall and deeply placed stomata. The pronounced palisade formation is indicated. $\times 300$.

d, Section of leaf of *Antizoma capensis* showing the superficially placed stomata and palisade chlorenchyma. $\times 300$.

e, *Galenia africana*, to show the vesicular epidermal cells, superficial placing of the stomata, and character of the outer chlorenchyma. $\times 300$.

f, Cross-section of branch of *Cadaba juncea* showing the deeply placed stomata with marked development of outer vestibule. The heavy character of the epidermis is indicated. $\times 300$.

g, *Cadaba juncea*, shoot, fragment of section taken immediately within the chlorenchyma to show the tracheids. $\times 300$.

h, Cross-section of leaf of *Grewia cana* showing the dorsi-ventral symmetry of structure. The heavy epidermis of the dorsal side, without cover trichomes, and the light epidermis of the ventral side with trichomes are shown.

i, *Grewia cana*, fragment of cross-section of ventral portion of leaf showing the superficially placed stomata. $\times 325$.

j, Fragment of cross-section of leaf of *Rhus viminalis*, to show excessive development of palisades. The thickness of the leaf is indicated. $\times 150$.

k, Detail of epidermis from ventral side of leaf of *Rhus viminalis* showing character of stomata, and suggestion that of the spongy chlorenchyma below it. $\times 325$.

l, *Rhus* sp. Whitehill. Fragment of epidermis from dorsal surface of leaf, to show the heavy covering of resin and its relation to the base of trichome. $\times 300$.

m, *Gymnosporia buxifolia*, detail of epidermis of leaf, longitudinal section, showing superficial placing of stomata and the fairly heavy outer walls. Cuboid sub-epidermal cells, in effect a hypoderm, separate the palisades from the epidermis. $\times 325$.

FIG. 8.

and larger leaf, about 11 cm. in length, was situated about midway between the youngest and the oldest leaves. The older leaf had a somewhat upwardly inclined position, while that of the younger leaf was nearly vertical. In the former case the dorsal and concave surface was fully exposed, while the ventral and convex surface was protected against the direct rays of the sun, but in the case of the younger and larger leaf the ventral surface was exposed and the dorsal surface was fairly well protected by the younger and inner leaves, as well as by the position itself.

A cross-section of the leaf shows a simple structure. For the most part, the tissue consists of large, cuboid cells, with prominent intercellular spaces, and without chlorophyll. A relatively narrow zone of chlorenchyma bounds the latter tissue on the outside. The innermost cells of the chlorenchyma are similar in form and size to the colorless mesophyll cells, but those nearer the epidermis are elongated somewhat in a direction at right angles to the surface of the leaf. They, however, are, properly speaking, not palisades.

The cell contents of both chlorenchyma and mesophyll stain with an alcoholic solution of safranin and probably contain mucilage in some form. Especial mucilage-bearing cells, however, were not observed.

In the older leaf the outer chlorenchyma was in large part crushed against the epidermis, giving much the effect of lifeless cork cells. Instances were observed, in this case, where the inner and thick (cellulose) layer of the outer epidermal wall was apparently wanting.

The epidermis of both the dorsal and the ventral surfaces is heavy, with an outer wall frequently more than one-half the entire diameter of the epidermal cell. The cuticle, and especially the portion of the outer wall which is cuticularized, is relatively thick (fig. 8A). The inner portion, which does not stain with safranin, constitutes most of outer wall.

Stomata occur on both leaf-surfaces and are deeply placed, owing to the great thickness of the outer epidermal wall. A canal leads through the outer epidermal wall to the guard-cells. This is somewhat restricted at the opening, which has a diameter of about 0.0076 mm. It was found that in many cases the canal was filled with a dark-colored substance, not soluble in cold alcohol.

ASPARAGUS STRIATUS.

The leaves of *Asparagus striatus* were studied from material collected on the lower northeast slope of a kopje near Beaufort West. The leaves are short and rigid, having the appearance of dwarf branches, and the dried plants, when properly treated for studying, present the essential structural points of the organ. Only dried plants were used.

The most striking anatomical features of the leaves are as follows: In cross-section the leaf is oval and the following are the most important tissues, concentrically arranged. The innermost mesophyll is composed for the most part of fairly thin-walled cells, cuboid in form. Outside this is a zone of sclerenchyma almost devoid of lumen, about equaling the chlorenchyma in thickness. There is then a zone of large cuboid cells, two or three cells in diameter, and either within or without this zone, somewhat over half the distance from the epidermis to the center of the leaf, occurs the region with conductive tissue. There also are thin-walled, parenchymatous cells, with cellulose walls, in the zone last referred to. With this exception, and as shown by reaction with chloroiodide of zinc, the walls of the tissues mentioned are lignified. Peripheral to these tissues lies the chlorenchyma, which consists of an outer layer, one cell in thickness, which is short-palisade in character, and an inner portion of cuboid cells. The chlorenchyma is in thickness about one-eighth the diameter of the leaf. On the ventral side of the leaf, however, palisade cells are quite wanting and the subepidermal layer of chlorenchyma is wholly cuboid.

Crystal aggregates, calcium oxalate, occur in the cells between the chlorenchyma and the supporting tissue within, and in the tissue with lignified walls and relatively large lumen contiguous to the latter.

Except in the palisades, intercellular spaces are wanting, or rarely present.

The epidermis is fairly heavy and the outer wall is heavy and heavily cuticularized. The deposition of cutin extends to the lateral walls, the outer portions, at least, of which give the reaction of this substance.

The stomata are somewhat deeply placed (fig. 8B) and the outer wall of the subsidiary cells is projected slightly, thus making at the same time the canal leading to the guard-cells somewhat longer, and the latter of a consequence somewhat deeper than if the outer wall of these cells were level with the general leaf-surface. The thin outer coating of the epidermal outer wall, the inner face of the stomatal canal, and the outer guard-cell ridges, which delimit the vestibule, and not shown in the sketch, color deep brick-red with chloroiodide of zinc, indicating that they are cuticularized.

It may be emphasized that the leading structural characteristics of the leaf are the large proportion of tissues of which the walls are lignified, the almost entire lack of intercellular spaces, and the large development of supporting tissue. These features make for rigidity of the leaf.

PROTEA NERIIFOLIA.

The material of *Protea neriifolia* which was examined was collected at Tweedside, about 13 miles west of Matjesfontein, and at a somewhat higher altitude. Owing to the presence of a relatively large amount

of mechanical tissue, as will be mentioned below, dried plants of the species answer fairly well for a cursory examination of the leaf anatomy.

Young as well as older leaves were studied. The latter measured about 2.8 by 8.3 mm. in size and the former was approximately half as large.

The mature leaves assume a fairly upright position on the shrub, of which the branches are upright also, but the younger leaves are more or less horizontally placed (plate 19B).

A cross-section of an old leaf shows that the structure is isosymmetrical.¹ Colorless parenchyma make up the middle of the leaf, and the chlorenchyma is composed of about two layers of relatively long palisades on either side.

Sclerenchyma occurs in connection with the fibro-vascular bundles, and in that position forms a prominent element of the leaf-tissues.

Crystals are fairly abundant in the outer layers of the mesophyll and in the inner ends of the innermost layer of palisade cells.

In the young leaf the epidermis is fairly light, and the outer wall, although thin, is, however, cuticularized. Cover-hairs with heavy walls are present in the young leaf. The epidermis of the old leaf is heavy, in part because of the much thickened outer wall. Trichomes are wanting.

Stomata occur on both surfaces of the leaves (fig. 8c). They are somewhat sunken, especially in the older leaves, and are provided with a canal which is nearly closed by the permanent constriction of the distal portion.

The leaf-surface is slightly roughened, possibly owing to the persistence of the very bases of the trichomes, which fall away as the leaf matures, and it is noticeable that the surface is free of any covering, as of wax.

ANTIZOMA CAPENSIS.

The twiner *Antizoma capensis* was collected at White Hills, and only dried material was available for examination.

The oval leaves, about 10 cm. in length, have the appearance of having unlike dorsal and ventral sides, although, as will appear directly, the symmetry is really dorsi-ventral.

The entire mesophyll and the chlorenchyma consist of relatively short palisades, a condition not common in the Menispermaceæ, according to Solereder, who reports it for *Cocculus laëba* only.² Apparently intercellular spaces are abundant, and of a consequence the cells are held but loosely together, from the fact that when the dried leaves are prepared by treating with hot water and by placing subsequently in 50 per cent alcohol with a small amount of glycerine, and are then

¹ A term here used to denote balanced structure in leaves.

² Systematische Anatomie der Dicotyledonen. Stuttgart, 1899, p. 45.

sectioned by hand, the entire mesophyll falls apart, and largely as separate cells.

The epidermis has a relatively heavy outer wall which is roughened into squat papilla-like projections. The lateral and inner walls are not appreciably thickened and apparently do not become mucilagenous. If present, a waxy coating of the epidermis is not heavy, and may be wanting.

Stomata occur on both leaf-surfaces and are not sunken below the general level of the leaf-surface (fig. 8D).

GALENIA AFRICANA.

The structure of the leaves was examined in material which was collected at Matjesfontein and put into a dilute solution of formaline while still fresh.

The leaves of *Galenia africana* vary from about 10 to about 20 mm. in length and are 1.5 mm., or less, in diameter, and are relatively thin.

A cross-section of the leaf presents a striking appearance. So many of the epidermal cells are developed into vesicles that cursory inspection suggests the entire epidermis to be composed of these cells. Such spherical epidermal cells, midway from side to side of the leaf, measure about 0.015 mm. as opposed to about 0.0012 mm., the diameter of a more common type, which have not developed in this manner (fig. 8E). It should be remarked, however, that in other species of the Ficoideæ the vesicular epidermals get to be the size of peas ("Erb-sengrösse"), according to Solereder.¹

The epidermal cells of the usual type are with thin outer walls. The outer walls of this form, however, as well as the vesicular epidermal cells, are possibly thinly cuticularized, as would be indicated by the reaction to chloroiodide of zinc, which stains the inner portion of such walls blue-violet and leaves the outer portion golden. A delicate covering of wax may be the final protection of the epidermal cells of both forms.

Two-armed trichomes, "cover" trichomes, are fairly abundant.

The stomata are on a level with the small epidermal cells and are well protected by the large spherical cells which arch above them.

The chlorenchyma consists of palisades, two or three cells in depth, which are relatively short, but are alike on the two sides of the leaf. In the innermost portion of the leaf and in association with the conductive tissue are large cuboid cells which do not contain chlorophyll and are probably to be regarded as functioning as water reservoirs.

Large spherical aggregates of crystals, calcium oxalate, occur in cuboid cells in the chlorenchyma, and especially in the innermost layer.

CADABA JUNCEA.

Specimens of *Cadaba juncea* were collected near Beaufort West in winter, when the rudimentary leaves which appear during the warm

¹ L. c., p. 469.

seasons were absent. The short branches with pointed ends, rush-like in appearance, are chlorophyll-bearing and carry on the leaf functions. The structure of such branches only was examined.

A cross-section of a chlorophyll-bearing branch shows a central woody portion with prominent medullary rays, and a cortex with well-differentiated outer and inner portion. A heavy epidermis is present, and stomata of which the guard-cells are parallel to the long axis of the branch.

Wood fibers are abundant in connection with the woody tissues and also occur in groups in the chlorenchyma as well.

The inner portion of the cortex is for the most part composed of cuboid cells well filled with starch. Toward the inner edge of the latter are separate groups of heavy-walled cells, long and with lumen, and along the outer portion, immediately within the chlorenchyma, are scattered tracheids (fig. 8F).

The chlorenchyma consists of greatly elongated, and hence relatively narrow, palisades in the inner half, of which the contents are noticeably more abundant than in the outer portion. Tracheids occur occasionally in the chlorenchyma, sometimes being in contact with the epidermis, and sometimes being wholly surrounded by the cells of this tissue (fig. 8G). The contents of the idioblasts take such stains and reagents as were used differently from the neighboring cells, and they may contain myrosin, although myrosin cells are not reported by Solereder as having been found in *Cadaba*.¹

The epidermal cells are much elongated radially, and the outer as well as the lateral walls are colored orange by chloriodide zinc, the inner wall only showing the reaction for cellulose.

The stomata are deeply placed, owing to the excessively heavy outer epidermal wall. The outer stomatal canal, of a consequence, is prominently developed. The ridges of the vestibule form a comparatively small opening to the vestibule, so that between the long canal, whose mouth is about 0.0026 mm. in diameter, and the vestibule, the entrance to which is even smaller, the stomata finds marked protection against excessive changes in the moisture content, more especially, of the enveloping atmosphere.

Both the chlorenchyma and the tissue just within contain crystals of various size and form, some prismatic, others oblong or square, and others six-angled. Whether crystals of calcium sulphate are to be found in the epidermal cells or in the chlorenchyma was not determined. The treatment of the material necessary for the structural studies would dissolve gypsum crystals, making their detection impossible. Such might be expected to be present, however, as it is known to be found in *Capparis jamaicensis* and other species of that genus. The crystals are mainly calcium oxalate.

¹ L. c., p. 84.

GREWIA CANA.

The shrub *Grewia cana* was one of the species used in field studies on the foliar transpiring power of perennials. It was collected at Beaufort West and only herbarium material was examined in the structural studies.

The leaves of *Grewia* are about 11 by 21 mm. in size and are fairly thin. They have well-marked upper and lower sides (plate 7B).

An examination of the leaf-structure shows that the meosphyll is of palisade cells throughout, although the cells of the ventral side are somewhat shorter and more stout than those of the side opposite. The difference, however, is not always so much as that indicated by the figure (fig. 8H). Intercellular spaces are especially prominent on the ventral side.

Supporting tissue, lignified fibers, occurs on either side, dorsal and ventral, of the fibro-vascular bundles, but it is not an especially prominent feature.

The epidermis of the dorsal side is relatively heavy with heavy outer wall. The contents of the epidermal cells stains violet with chloroiodide of zinc, indicating the possible presence of mucilage.

The epidermal cells of the ventral side are somewhat smaller and the outer wall not so heavy as in the case of the dorsal epidermal cells.

The stomata, which do not appear to be abundant as in many species, are confined to the ventral side. The guard-cells are raised somewhat above the general level of the leaf-surface (fig. 8I), as commonly is the case where the leaf is provided with a permanent covering of trichomes.

Stellate and appressed trichomes occur thickly on the ventral side and constitute an almost continuous cover. The rays of the trichomes appear always to be unicellular and never to consist of a chain of cells, as Solereder reports has been found in some species.¹

RHUS VIMINALIS.

The leaves of *Rhus viminalis* which were examined were from a tree growing at Matjesfontein which had been used in the studies on the foliar transpiring power. Dried material only was available for the anatomical work.

The leaves of this species of *Rhus* have leaflets 85 mm., more or less, in length, and about 8 mm. in width. The slender leaflets which hang vertically and the drooping habit of many of the branches of the tree give the appearance of species of *Salix* (plate 20A).

A cross-section of the leaflet shows marked dorsi-ventrality (fig. 8J). Greatly elongated palisade cells reach from the dorsal epidermis to about the middle of the leaf. The palisade tissue is continued somewhat further by somewhat shorter palisades. On the ventral side,

¹ *L. c.*, p. 178.

spongy tissue extends to a depth approximately one-fourth the diameter of the leaf. Intercellular spaces are largely wanting on the dorsal side, but are plentiful on the ventral side.

Sclerenchyma occurs in connection with the fibro-vascular bundles, as well as along the margins of the leaf.

Sections across the conductive tissue show the presence of ducts in the phloem. Whether by anastomosing the ducts form a network, as in certain species of *Rhus*, was not determined.

The epidermis is not very heavy, although the outer wall, especially of the dorsal side, is relatively thick.

Stomata are to be found only on the ventral side and are not deeply placed (fig. 8K).

Shield-shaped secreting trichomes are sparingly present on both surfaces of the old leaves.

RHUS SP.

Rhus sp. was used in studies on the foliar transpiring power at the Karroo Botanical Gardens, Whitehills, and dried leaves of the plant so used were examined anatomically.

It should be remarked in passing that the habitat of this species at Whitehills is the rounded summit of a kopje, where it occurs in association with *Euclea* sp. The environment of the species is very much more arid than that of *Rhus viminalis*, which occurs along the streamway at Matjesfontein, at which place the rainfall is also greater.

The leaflets vary in form from obcordate to oblong-linear and in size from about 5 to 10 mm. in width and from about 10 to 30 mm. in length.

The leaf-structure of *Rhus* sp. resembles that of *Rhus viminalis* in the fundamental points, but it is very different in certain features respecting the degree of development of certain of the tissues.

As in the case of *Rhus viminalis*, the structural symmetry is dorsiventral. Palisades occur on the dorsal side and spongy chlorenchyma on the ventral side. Stomata occur on the ventral side only and are not sunken deeply, but are about on the general level of the surface of the leaf. Sclerenchyma occurs along with the conductive tissue, and ducts are present. When examined more closely, however, each of these tissues has a character different from that of the corresponding tissue in the other species.

The outer epidermal wall on the dorsal surface is not especially thick, but it is at least in part covered by a heavy mass of resinous substance apparently secreted by trichomes (fig. 8L). This feature is quite as well marked on the ventral side, where irregularities in the surface of the leaf are quite filled by the resin, a feature wanting in the leaves of *Rhus viminalis* examined.

The chlorenchyma of *Rhus* sp. is in part palisades and in part composed of cuboid cells, both with small intercellular spaces, and of

spongy parenchyma. The outer layer of palisades is about 0.07 mm. in length as contrasted to the corresponding palisades of *Rhus viminalis*, which measure about 0.4 mm., and make up about one-fifth of the chlorenchyma. From this it will appear that the relative amount of palisade tissue in *Rhus* sp. is much less than that of the other species.

Supporting tissue is associated with the fibro-vascular bundles, but it is not so pronounced a feature as in *Rhus viminalis*. On the other hand, the ducts which occur in the phloem of the fibro-vascular bundles are very much larger than in *Rhus viminalis*.

GYMNOSPORIA BUXIFOLIA.

Gymnosporia buxifolia was used at Beaufort West in connection with studies on the foliar transpiring power of some of the Karroo perennials. This species, according to Bews,¹ is somewhat variable and is widespread all over South Africa. It is very spiny in the drier situations. The general habit of the species and the character of the leaves are shown in the illustrations (plate 7c and plate 7A). It will be seen from the figures that, although not large, the leaves are abundant and their positions bears apparently no especial relation to the incident light rays.

A cross-section or a longitudinal section of a typical mature leaf shows several striking features. The epidermis, with heavy outer wall, nearly obliterating the lumen, is underlaid by one or two layers of cuboid cells, beneath which is the chlorenchyma proper. Schlerenchyma occurs in association with the conductive tissue. Stomata are numerous and are to be found on both surfaces of the leaf. They are level with the outer epidermal wall, or even project somewhat. There is little or no external vestibule and the substomal chamber is small (fig. 8M).

The walls of the hypoderm and the inner and lateral walls of the epidermis are light. Although in older leaves the hypodermal cells are apparently without contents, for the most part there are occasional cells of this tissue which contain crystal aggregates which nearly fill them. Similar secretion cells, with calcium oxalate crystals of the same appearance, occur in the chlorenchyma as well. In the middle of the leaf the chlorophyll-bearing cells are cuboid, or may even have the long axis parallel to the leaf-surface, but for the most part the chlorenchyma consists of short palisades. Intercellular spaces are apparently but poorly developed.

CUSSONIA SPICATA.

The material, which was studied in the dried condition, was collected on the upper north face of a flat-topped and low mountain

¹The Southeast African flora: Its origin, migrations, and evolutionary tendencies. Ann. Bot., 36, 216, 1922.

near Beaufort West, where it occurs sparingly. The large palmate leaves of the plant, which are borne only at the summit of the branches, give a subtropical appearance, somewhat out of keeping with the remainder of the vegetation of the vicinity.

The leaves of *Cussonia* are about 32 by 160 mm. and are of a leathery texture. They are distinctly bifacial in appearance.

The most striking single characteristic of the structure of the leaf is the presence, on the dorsal side only, of a hypoderm consisting of three or four layers of cells. Between the veins the cells of this tissue are cuboid, but opposite the fibro-vascular bundles they are somewhat elongated. On both sides of the leaf, and in relation to the conductive tissue, thus dorsal and ventral as well, the hypodermal cells constitute the entire issue to the epidermis. This condition is at least true of the larger "veins." It will be seen, therefore, that the supporting tissue is unusually well developed in the species and that to a degree the chlorenchyma is separated into separate masses. The general character of the hypoderm is given in figure 13A.

The true epidermis of the dorsal side of the leaf is not especially heavy, although the outer wall is very thick and has a much thickened cuticle. That of the ventral side is also heavy and projects into short papillæ, giving to the surface, when viewed under a microscope, a somewhat roughened appearance. The dorsal leaf-surface, on the other hand, is fairly smooth. The epidermal cells of the ventral side have granular contents, the nature of which was not investigated, while the dorsal epidermal cells appear to be entirely empty.

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- FIG. 9.—*a*, *Cussonia spicata*, detail of epidermis, showing stomata, and cuboid chlorenchyma. Ventral surface. $\times 300$.
b, *Cussonia spicata*, dorsal surface of leaf, showing heavy outer epidermal wall and hypodermis, several cells in thickness, with palisades within. $\times 300$.
c, Fragment of leaf of *Cotyledon paniculata*, prepared from material grown at the Coastal Laboratory, showing the cuboid chlorenchyma and delicate epidermis. $\times 70$.
d, Cross-section of leaf of *Stachys* sp., showing the confused mass of trichomes on both surfaces and the prominently developed palisades on the dorsal side, with spongy parenchyma on the ventral side and stomata with guard-cells which project slightly. $\times 300$.
e, *Aptosimum indivisum*, cross-section of leaf, showing heavily developed outer epidermal wall, short palisades, and superficially placed stomata. $\times 300$.
f, *Carissa ferox*, fragment of ventral side of leaf showing heavy outer epidermal walls, with superficially placed stomata, having two subsidiary cells. The palisade-like character of the outer chlorenchyma of the ventral side is indicated. There probably are better developed intercellular spaces, however, than are shown in the sketch. $\times 325$.
g, *Asclepias filiformis* (?), semi-diagrammatic cross-section of leaf, showing channelling of leaf and disposition of main tissues. The two separate masses of chlorenchyma are indicated. For further explanation, see text. $\times 70$.
h, *Asclepias filiformis* (?), detail from dorsal side of leaf, showing the heavy outer epidermal wall and character of stomata. $\times 300$.
i, *Euclea undulata*, fragment of cross-section of ventral side of leaf, showing the superficial placing of the stomata and character of the epidermis. $\times 300$.
j, *Euclea undulata*, portion of cross-section of leaf to show the heavy epidermis, prominent development of palisade cells, and sclerenchyma. $\times 300$.
k, *Eriocephalus* sp., cross-section of leaf, with the most prominent tissues outlined: *e*, epidermis; *fv*, conductive tissue; *p*, chlorenchyma. $\times 225$.

FIG. 9.

Stomata occur on the ventral side only and are not sunken, but are about level with the leaf-surface (fig. 9B).

Secreting ducts occur in relation to the phloem of the fibro-vascular bundles and are not found in the chlorenchyma.

The chlorophyll-bearing tissue is in part of poorly developed palisades and in part of spongy parenchyma. The former are about four cell layers deep and lie immediately beneath the hypoderm, and the latter are on the ventral side. Intercellular spaces are more abundant in the latter than in the former type of chlorenchyma, although apparently not a pronounced feature of either.

BAUHINIA MARLOTHII.

Bauhinia marlothii was collected in the habitat of *Welwitschia mirabilis* in the Namib. Scattered along the same shallow depression in the desert plain were *Asclepias filiformis* and *Zygophyllum stapfii* (plate 3). Only dried material was available for the anatomical investigation, which, for reasons to appear directly, was not entirely satisfactory.

The leaflets examined were orbicular in form, fairly abundant, and and did not suggest the extreme aridity of the habitat. The following were the most striking points in the structure of the leaves. Except for the usual dorsi-ventral arrangement of the conductive system, the structure of the two sides of the leaf is alike. That is, palisade cells similar in form occur both on the ventral and the dorsal side, with cuboid parenchyma between. Stomata occur on both surfaces of the leaf. Trichomes were not found and sclerenchymatous tissue of any kind is wanting. It is owing to the last-named circumstance that, as suggested above, dried material is not suitable for anatomical study of the leaf.

In the young leaf the epidermal cells are relatively large, and in age these cells enlarge greatly and become almost vesicular. The outer walls, which are relatively thin, are therefore markedly convex. The stomata in the old leaf are superficially placed, and, although fairly numerous, appear, as compared to those of many species, to be of small size.

SUTHERLANDIA FRUTESCENS.

The material of *Sutherlandia frutescens* used in the anatomical study was collected near a streamway about 6 miles east of Beaufort West, where it occurs together with *Senecio longifolius*, *Mesembryanthemum unidens*, and other perennials. As stated elsewhere in this paper, the habitat is apparently less arid than Beaufort West, holding also somewhat different relations to the mountains.

Although the material at hand was not very satisfactory for anatomical study, it was possible to make out the following general struc-

tural features of the leaflets. The mesophyll is of palisade cells throughout with intercellular spaces apparently well developed. Stomata occur on both surfaces and, at least in the young leaves, there is a sparse covering of non-secreting trichomes. The epidermis, both of the dorsal and the ventral sides, is fairly heavy. Supporting tissue of whatever kind, that is to say sclerenchyma, is absent.

COTYLEDON PANICULATA. .

Cotyledon paniculata, which is one of the most striking species with water-storage capacity in southern Africa, has a stout stem and heavy, short branches (plate 18B). The leaves are formed in early autumn and persist through the winter months and into the spring, until the advent of warm and dry weather. Then they fall and the summer is passed with only such carbon-dioxide assimilation as may be possible on the part of the green branches.

Studies on the transpiring power of the leaves of this species were carried out at Matjesfontein.

The plants used in the anatomical study were collected at Matjesfontein and came into leaf, following irrigation, in early summer. Leaves from small plants were studied in the fresh condition.

The leaves used measured about 80 by 35 mm. and had a thickness of about 2.5 mm.

The leaf has the general structure of leaves of succulents. It is mechanically weak. The epidermis is light and is easily stripped in ribbons from either surface. The chlorenchyma is of cuboid parenchyma only and has abundant intercellular spaces. Even in the middle of the leaf chlorophyll is present in abundance. There is no supporting tissue and the conductive system appears to be meager. Glandular trichomes occur on both surfaces (fig. 9c). The mesophyll cells are highly mucilaginous and, although quite turgid when placed in water, they nevertheless increase in thickness appreciably and the leaf usually exhibits curving, but apparently only in a certain direction. Whether, however, the dorsal surface uniformly becomes concave under such conditions, as in the young plant, was not learned.

The outer epidermal wall of both leaf-surfaces in the material used was found to be thin, and of a consequence the stomata, which occur on both sides of the leaf, are not sunken. The stomata are relatively not abundant. For example, it was found that per unit area there were approximately twice as many stomata on the ventral side of a sunflower leaf as was counted in *Cotyledon*. Whether, however, the same would be true for a corresponding specimen growing on the veld at Matjesfontein, I have no means of finding out. The findings are opposed to the usual experience that for the same area the number of stomata is greater in xerophytes than in mesophytes.

STACHYS SP.

The species of *Stachys* studied, of which only dried material was available, was collected on the south side of a canyon about 6 miles east of Beaufort West, at a place where the vegetation was relatively abundant, both as to the number of species and individuals. Among other forms the following perennials were found in the vicinity: *Cussonia spicata*, *Cadaba juncea*, *Eriocephalus* sp., *Euclea undulata*, and *Pteronia incana*.

The leaves measured 15 by 20 mm. or less in size and are markedly bifacial and otherwise have the general character of the family. In section they exhibit the following main structural features: The leaf is relatively thin. The conductive tissue is well developed and constitutes the main supporting system. Heavy-walled mechanical tissue appears to be quite absent. The structural symmetry is strongly dorsi-ventral. Both leaf-surfaces are very heavily clothed with cover trichomes. The stomata are confined to the ventral surface.

When examined somewhat in greater detail, it is found that the epidermis is not heavy and the outer wall is thin. Apparently every epidermal cell, or by far the most of them, of the dorsal side gives rise to a trichome. The same is also true, but possibly to a somewhat less extent, of the cells of the ventral epidermis (fig. 9D). The trichomes are so abundant as to form a felted covering to the leaf. This remark refers especially to the young leaf. In age, possibly because of the increase in size of the epidermal cells, and possibly also because of the shedding of some of the trichomes, the pubescence appears not to be so dense. In such leaves epidermal cells can more easily be made out between the trichomes. In a section of a leaf where the trichomes remain it is found that the felted trichomal mass of either leaf-surface exceeds the diameter of the main part of the lamina itself.

The stomata are placed so that they not only are not depressed below the general level of the leaf, but on the contrary the guard-cells are noticeably elevated. As will be commented on elsewhere in this paper, this condition has been found to be the frequent or possibly the invariable accompaniment of pubescence of the leaf.

APTOSIMUM INDIVISUM.

Aptosimum indivisum was collected on the northern exposure of a dolorite kopje near Beaufort West, where *Euphorbia mauritanica*, *Pentzia virgata*, and *Asparagus striatus* also occur. Leaves of the rosette, and dried material only, were used in the anatomical study.

The rosette leaves are about 6 by 20 mm. in size and have the appearance of being bifacial. They are clustered thickly on the shortened stem and do not appear to have especial orientation.

In cross-section the leaf is found to have a very simple structure. The mesophyll is of short palisades throughout. Stomata occur on both surfaces. Sclerenchyma is but little developed, only accompanying the fibro-vascular bundles. The outer epidermal wall is of great relative thickness and apparently constitutes the leading mechanical element of the leaf.

In the material studied trichomes were not present, so that it was somewhat surprising to find the guard-cells slightly elevated above the epidermal cells proper, although, owing to the heavy outer epidermal wall, they are slightly below the general level of the leaf (fig. 9E).

The ridges of the outer vestibule are prominently developed, in fact more so than is indicated by the figure.

The outer surface of the epidermal wall is slightly ribbed, giving the leaf-surface fine striations. The cuticle is light.

CARISSA FEROX.

The material of *Carissa ferox* which was used in the anatomical study was from quadrat No. 1, on the southern slope of a dolorite kopje near Beaufort West. It was associated with *Euphorbia mauritanica*, *Grewia cana*, and other perennials (plate 8c). The species is intensely spiniferous. The smaller branches and spines, at least, are chlorophyll-bearing. The oval leaves are about 10 by 25 mm. in size, are relatively thick, and leathery in texture.

Dried material only was available for the study of the leaf-structure. A general view of the anatomy shows the following important features: The structure is dorsi-ventral, although the tendency of the chlorenchyma of the ventral side toward palisade form may be noted. Throughout the central portion of the leaf and only in part directly connected with the fibro-vascular bundles is to be found the lactiferous tissue. Sclerenchyma is present in connection with the conductive tissue, but apparently only in association with the xylem elements. The epidermis, especially of the dorsal side, is heavy, because of the extremely thick outer wall. Trichomes are sparingly present on both leaf-surfaces, and where they take their origin the lumen of the epidermal cell is somewhat larger than that of the contiguous epidermal cells, from the fact that the inner secondary thickening of the outer wall in such cells fails. This condition results in a circular and narrow band at the base of each trichome where the "protection" against possible water-loss, such as that afforded the outer leaf cells by the thicker neighboring outer epidermal wall, is to a certain extent wanting. The stomata occur only on the ventral side. They are about flush with the general level of the leaf-surface. There are two subsidiary cells (fig. 9F).

ASCLEPIAS FILIFORMIS (?).

The material of *Asclepias filiformis* (?) which was used in the anatomical studies was collected in the habitat of *Welwitschia mirabilis* in the Namib. Owing to the extreme aridity of the habitat, more than usual interest attaches to the peculiarities of the species which can survive its rigors. Among such are, in addition to those above mentioned, *Arthrærua marlothii* and *Zygophyllum stapfi*. Although exposed to a common environment, these species have nevertheless developed in different directions, all being perennials. The general character of the species need only be mentioned in this place. That of *Welwitschia* is well known. This species has a well-developed tap-root with large crown which may act in the capacity of storage organ for water. *Asclepias* has apparently no storage capacity, while the branches of *Arthrærua* are somewhat fleshy (plates 4A and 5B), and the leaves only of *Zygophyllum* are succulent (plates 2c and 3c).

Dried material only was used in the anatomical study. The leaves are strap-shaped but exceedingly long. Although both old and young leaves were examined, this report refers mainly to a leaf measuring 2.5 by 150 mm. A cross-section of such a leaf shows three main regions, namely, a central region dominated by the midrib, and two lateral regions wholly separated by the midrib. The latter consist of chlorenchyma in the midst of which are several small fibro-vascular bundles. The latter are not indicated in the general sketch of the tissues of the leaf (fig. 9G). As the figure shows, the leaf is strongly channeled with two grooves on the ventral side and one opposite their intersection on the dorsal side.

The tissues of the midrib region consist of the fibro-vascular bundle, of which the vascular part is very pronounced, being composed in outline of the V-shaped mass of the figure referred to, and two masses of cuboid cells toward the leaf-surfaces. Of these, that dorsal to the conductive tissue is wholly of thin walls and contains a half dozen or more lactiferous ducts; but on the opposite side the corresponding cells are with heavy walls near the leaf-surface and with light walls nearer the fibro-vascular bundle. None of these cells bears chlorophyll. Their walls are not lignified, but with zinc-chloroiodide give the reaction for cellulose. Intercellular spaces are present in the cuboid tissue of either side, except only for the most part in that with heavy walls, where they appear to be wanting.

As indicated above, the tissue containing chlorophyll consists of two ribbon-like masses running lengthwise of the leaf and wholly separated from each other. On the dorsal side the chlorenchyma is of palisades and on the ventral side it is of spongy parenchyma.

Stomata occur sparingly on both leaf-surfaces, as indicated diagrammatically in figure 9G. They are placed superficially (see figure

9H), which is somewhat to one side of the median line of the stoma, and do not have pronounced outer ridges or vestibule.

The epidermis has a heavy outer wall opposite the chlorenchyma and is overlaid with a coating of wax, not only in the portion associated with the chlorophyll-bearing cells, but opposite the midrib as well.

The point should be brought out in passing that there is no heavy-walled supporting tissue in the leaves. In the slender stems, however, such is to be found. This is in the primary cortex, where there is a ring of hard bast composed of bundles separated from each other by a radial layer of parenchyma. It is largely to this mechanical tissue that the rigidity of the stem is due.

EUCLEA UNDULATA.

The material used in the anatomical study was collected about 6 miles east of Beaufort West. In the same habitat were numerous other perennials, among which were *Cussonia spicata*, *Cadaba juncea*, *Eriocephalus* sp. and *Pteronia incana*, of which the leaf-structure was studied, and others. Observations on the foliar transpiring power of *Euclea undulata* were carried out at Matjesfontein.

Euclea undulata is a large shrub. The evergreen leaves are numerous and relatively large, measuring about 20 by 30 mm. or less, and are confined to the tips of the branches. Both young and old leaves were examined, with the following results: The structure is dorsiventral. Trichomes are abundant on both leaf-surfaces. Stomata are confined to the ventral side. There is marked development of supporting tissue.

Trichomes of different types, some of which are glandular, are especially abundant in the younger leaf. A correlation between light outer epidermal wall and the presence of trichomes, and of a heavy outer wall where they are wanting, was noted.

The outer wall of the epidermis, both of the ventral and of the dorsal sides, is very heavy and the cuticle well developed. The inner epidermal wall also is heavy (fig. 9I). The stomata do not appear to be very abundant and are not sunken appreciably below the general level of the leaf.

The chlorenchyma consists of about one cell-layer of palisades, with the balance cuboid cells or spongy parenchyma. In the latter case intercellular spaces are abundant.

Sclerenchyma occurs both on the dorsal and the ventral sides of the conductive tissue, and between them and the epidermis. That in connection with the midrib is especially heavy (fig. 9J). Exterior to the strand of sclerenchyma and connecting it to the epidermis of either surface are masses of heavy-walled cuboid cells, which are apparently without contents in age. This refers to the midrib. Apparently in the smaller fibro-vascular systems such tissue is wanting.

ROYENA PALLENS.

The material of *Royena pallens* studied was collected on the lower slopes of a kopje about 2 miles or less from Beaufort West. The character of the habitat is shown in plate 6B. The leading species of the general habitat are listed at page 66.

The leathery leaves are 2 mm., more or less, in length and 6 mm., or less, in width. They have distinct upper and lower faces.

A cross-section of mature leaves shows the following leading structural characters: The epidermis, which is not very heavy, is composed of relatively small cells. The outer wall is heavy and its outer portion is cuticularized. The surface of the cuticle is striated. Cover trichomes are apparently abundant in young leaves, but in old leaves they are largely wanting. They occur on both surfaces. Stomata are present on the ventral side only and are not sunken below the general level of the surface (fig. 10G). The chlorenchyma consists of palisades only, which are not alike on both sides of the leaf. Those of the ventral side are somewhat less palisade-like and the intercellular spaces of this side are apparently somewhat more abundant. The tissue of the middle part of the mesophyll is parenchyma with prominent intercellular spaces. The walls are of cellulose. A portion of the cells contains very large single crystals. Sclerenchyma is not present, either in connection with the fibro-vascular bundles or elsewhere.

ERIOCEPHALUS SP.

Eriocephalus sp. was observed at Matjesfontein, where the material studied was collected. It constitutes one of the population of quadrat

- FIG. 10.—*a*, *Eriocephalus* sp., cross-section of leaf, to show the absence of lumen in the epidermal cells because of the secondary thickening of the walls. The bases of two trichomes are shown, and the pronounced development of palisades indicated. $\times 300$.
- b*, *Euryops lateriflorus*, section of leaf in which the heavy epidermis, deeply placed stomata, and short palisades are indicated. $\times 300$.
- c*, *Pentzia virgata*, cross-section of leaf to show the superficially placed stomata, relatively thin epidermis with heavy outer wall, secreting trichome, and two-ranked palisade tissue. $\times 300$.
- d*, *Pteronia flexicaulis*, cross-section showing the distribution of the following tissues: *o*, epidermis; *fv*, conductive tissue with sclerenchyma in circles; *p*, chlorenchyma. $\times 150$.
- e*, *Pteronia flexicaulis*, cross-section showing the heavy epidermis with greatly thickened outer wall and superficially placed stomata. $\times 300$.
- f*, *Pteronia incana*, cross-section of leaf, in which the following are shown: *f*, duct; *fv*, conductive issue; *p*, chlorenchyma with the epidermis without the dotted line. $\times 50$.
- g*, *Ptergonia incana*, cross-section of leaf, showing heavy outer epidermal wall and relatively short palisades. $\times 300$.
- h*, *Royena pallens*, cross-section of leaf secretion on the surface of the epidermis, the superficially placed stomata, and palisades. $\times 300$.
- i*, *Stæbe* sp., semi-diagrammatic cross-section of leaf, showing the extent of the mass of trichomes on the ventral side, within the curving broken line, the width of the epidermis and the conductive tissue having sclerenchyma, indicated by circles, on either side. $\times 60$.
- j*, *Stæbe* sp., cross-section of leaf, showing modified dorsi-ventral symmetry of structure. The light epidermis, stomata with projecting guard-cells, and trichomes of the ventral side are sharply contrasted with the heavy epidermis, the absence of stomata and of trichomes of the dorsal side. $\times 300$.

FIG. 10.

No. 3, where it occurs in association with *Aster filiformis*, *Cotyledon orbiculata*, *C. reticulata*, *Pteronia glomerata*, *Stæbe* sp., and other forms.

The leaves of this species are terete in cross-section and about 6 mm. in length. They are borne in groups, frequently opposite, and usually on dwarf shoots.

A section of a leaf shows a prominent epidermis, a band of chlorenchyma, of palisades without, and fibro-vascular bundles with prominent masses of supporting tissue (fig. 13K). Cover trichomes are especially abundant in young leaves, arising from nearly every epidermal cell.

A most striking structural feature of the leaf is the epidermis, in which, because of the excessive thickness of the walls, the lumen is quite obliterated. The differential staining obtained with chloriodide of zinc is of interest. The bases of the trichomes and outer portion of the outer wall become orange, being cuticularized, while the greatly thickened walls otherwise become deep violet with this reagent.

The stomata are fairly deeply placed (fig. 10A), having the thickness of the epidermis between the guard-cells and the leaf-surface. In the development of the subsidiary cells, which are modified like the balance of the epidermis, there has been left no especial constriction of the stomatal pore, as was observed in other species, and outer ridges as well as vestibule appear to be quite wanting. Whether such are present in young leaves, however, as may have been the case, was not determined. As indicated by the orange color following the use of chloriodide of zinc, the outer portion of the walls of the guard-cells, to a point slightly within the stomatal chamber, is cuticularized.

The chlorenchyma consists of palisades, rather narrow and long. Within this tissue are elongated but wide cells which are radially disposed, and again within the last are cuboid cells. The last are not chlorophyll-bearing. The walls are fairly heavy and there are numerous intercellular spaces. Sclerenchymatous fibers are present on either side of the fibro-vascular bundle, that on the ventral side being especially well developed.

EURYOPS LATERIFLORUS.

Euryops lateriflorus, one of the species used in the studies on the transpiration power of leaves, was collected by a streamway at Matjesfontein. The habit of the species is shown in plate 10B.

Dried material only was used in the anatomical study. The coriaceous leaves are about 6 by 15 mm. in size. They are fairly abundant and are appressed to the upright branches.

An examination of the leaf in cross-section shows the following noteworthy features: The epidermis has a very much thickened outer wall. The palisade tissue, which is similar on both sides of the leaf, extends to the middle of the leaf and abuts on one or two layers of

thick-walled cuboid cells. Rather small groups of sclerenchyma occur in connection with the fibro-vascular bundles, particularly the larger ones, and on the ventral side. Surrounding the conductive tissue, and in the larger bundles between it and the dorsal epidermis, are thick-walled cuboid cells. Large canals, possibly resiniferous, are scattered through the chlorenchyma, mainly, however, appearing on the ventral side of the supporting tissue, or, when this is wanting, in association with the phloem. The extremely heavy outer epidermal wall, together with the occasional strands of sclerenchymatous fibers, account for the leathery texture of the leaves.

Stomata occur on both surfaces of the leaves. The guard-cells are deeply sunken and the walls lining the outer stomatal tube, together with the outer walls of the guard-cells, are heavy and probably cuticularized, as indicated by reaction with the use of an alcoholic solution of chlorophyll, staining deep green. The opening of the outer stomatal tube is much constricted, and the outer vestibule ridges are well developed, so that the approach to the stomata is guarded by small pores of fixed diameter (fig. 10B).

PENTZIA VIRGATA.

Pentzia virgata was collected at Matjesfontein, where it occurs abundantly on the veld. It was found to be dominant, with *Mesembryanthemum spinosum*, in quadrat No. 4, the vegetational character of which is shown in plate 21A.

The leaves of *Pentzia* are about 1.5 mm. in length and are terete. They occur in groups of four or more on dwarf shoots, 4 mm., more or less, in length, and are abundant.

The main structural features consist of an epidermis with relatively heavy outer wall, and trichomes, both cover trichomes and glandular ones, and a mesophyll of which the outer layers are palisades and the inner are cuboid cells. The former only contain chlorophyll. Glandular ducts are sparingly present in the mesophyll.

The stomata occur on each surface of the leaf and are about flush with the general level of the epidermis (fig. 10c). In young leaves both secreting and non-secreting trichomes are abundant, but in the older leaves the latter drop away.

PTERONIA FLEXICAULIS.

The material of *Pteronia flexicaulis* used in this study was collected at Matjesfontein in quadrat No. 4, where it occurs with *Mesembryanthemum spinosum*, *Pentzia virgata*, *Pteronia incana*, *Crassula columnaris*, *Asparagus capensis*, and others (plate 21A). The leaves, or leaf-like branches, are filiform, measuring about 1 by 30 mm. They are somewhat rigid.

The leading features of the anatomy can be briefly presented (fig. 10D). The epidermis is heavy because of the extremely thick outer wall.

The stomata are not noticeably sunken, but are fairly flush with the general level of the leaf-surface (fig. 10E). Trichomes are present. The chlorenchyma is of palisades and in diameter about equals one-eighth of the cross-section of the leaf. With the chlorenchyma is a central mass of cuboid cells in which are numerous fibro-vascular bundles, associated with which are heavy strands of sclerenchyma. Supporting tissue also appears to be present, unaccompanied by fibro-vascular bundles wholly within the chlorenchyma.

PTERONIA INCANA.

Pteronia incana was collected at Matjesfontein in quadrat No. 4, where it occurs with other species mentioned in the previous paragraph and the general character of which is shown in plate 31B. Dried material only was used in the anatomical examination.

The leaves occur in groups of a half dozen or more and measure about 1.5 by 7 mm. When young they are terete in cross-section, but when mature they are somewhat flattened.

A semi-diagrammatic section of an old leaf, such as represented by figure 10F, shows several main structural features, including heavy epidermis, ducts (*d*), palisade chlorenchyma (*p*), a non-chlorophyllous mesophyll of relatively few but large cells, and four or more strands of conductive tissue (*fv*).

When viewed somewhat more closely, it is seen that the conductive tissue is accompanied by strands of heavy-walled fibers which are especially prominent in association with the midrib of the leaf, and, among other features, that the palisades are not long cells and the chlorenchyma may be one to three cell-layers wide. Stomata are numerous on both surfaces and are not deeply placed (fig. 10G). The outer wall of the epidermis is very heavy. The outermost part of the wall is cuticularized, but for the most part it appears to be cellulose, as would be indicated by the reaction to chloroiodide of zinc. Trichomes are abundantly present in young leaves, but are largely wanting in those that are mature. There are both cover and glandular trichomes, of which the latter appear to persist the longer of the two.

RELHANIA SQUARROSA.

Relhania squarrosa is a shrub common on the veld in the vicinity of Matjesfontein. The branches are strict and well covered with small, saddle-shaped and somewhat recurved leaves. They stand out on the older parts of branches nearly at right angles to the branch, but on the younger parts they may be appressed to the branch. There thus is a distinctly ventral or lower side as opposed to the distinctly upper or dorsal side, with respect to the position of the branch, and hence with regard to such environmental features as the direction of the impinging rays of light. Such features would appear to be associated with a dorsi-ventral structure.

The leaves are about 4 by 8 mm. in size. An examination of a cross-section shows the leaf to have the following leading structural features: The epidermis has a very heavy outer wall of about the same thickness on either side of the leaf. Glandular trichomes occur on both dorsal and ventral sides, but sparingly. Where they take origin the outer epidermal wall, as is usually the case, is not thickened, so that the trichomes have the effect of being somewhat sunken in the leaf. Stomata occur both on the dorsal and the ventral side and are nearly or quite flush with the general level of the surface of the leaf. The chlorenchyma of both dorsal and ventral sides consists of palisade cells of a similar appearance. Sclerenchyma, which is often to be found in connection with the conductive tissue in the leaves, appears to be quite wanting, so that the leathery character is largely owing to the heavy outer epidermal wall in addition to the fibro-vascular bundles.

It would appear from the foregoing that the bifacial appearance is not carried out in the structure of the leaves.

STÆBE SP.

The material of *Stæbe* sp. used in the anatomical study was collected about 0.5 mile west of Matjesfontein, where it occurs in association with several other perennial shrubs, including, among others, *Aster filifolius*, *Cotyledon* sp., *Eriocephalus* sp., and *Pelargonium* sp.

The leaves are numerous but small, measuring about 1 by 10 mm., and occur in groups of a half dozen or more. The young leaves are somewhat folded, so that the surfaces on either side of the midrib, dorsal side, approximate one another.

In cross-section the leaf shows marked structural characteristics. On the ventral side cover trichomes occur in great abundance, forming a felt whose situation and extent are indicated diagrammatically in figure 10i. They are apparently never so abundant on the dorsal side, and in the mature leaves they are mainly wanting on that side, although still remaining on the ventral side. The epidermis on the dorsal side has a very heavy outer wall, while that of the opposite side is light. In the former instance, through secondary thickening of the wall, as was found to be the case in *Eriocephalus* and shown in figure 10j, the lumen of the cells of that side has nearly or wholly disappeared. Stomata are to be found only on the ventral side and present the peculiarity of having the guard-cells sharply projecting above the level of the leaf. The chlorenchyma is of palisade cells throughout, although that of the ventral side is possibly to be more accurately described as being palisade-like, inasmuch as the cells are not so long, or at least relatively more stout than the corresponding cells of the other side. Between the dorsal and the ventral chlorophyll-bearing cells, and hence in the middle of the leaf, are about two

layers of cuboid cells which do not contain chlorophyll. Sclerenchyma is strongly developed in relation to the conductive tissue, and is especially heavy on the ventral side of the bundles.

GENERAL SUMMARY AND DISCUSSION OF LEAF-STRUCTURES.

Although the list of species of which the foliar structure has just been passed in review is not a long one, the number of families represented is considerable. They are as follows: Liliaceæ, Proteaceæ, Menispermaceæ, Alizocæ, Capparidaceæ, Tiliaceæ, Anacardiaceæ, Celastraceæ, Araliaceæ, Leguminosæ, Crassulaceæ, Labiataë, Scrophulariaceæ, Asclepiadaceæ, Apocynaceæ, Ebenaceæ, and Compositæ. A glance at the list of species observed during the course of the reconnaissance of the plants of the more arid portions of southern Africa, given on page 10, will show that the list of families represented by the species observed might have been considerably extended. Although not to have done so is to be regretted, it was not feasible from the fact, as suggested before, that many of the forms did not have sufficient supporting tissue to satisfactorily maintain the structures for studies of an anatomical nature, which were largely carried on with dried material. When there is a relatively large amount of tissue with heavy walls present, especially fibrous tissue, the implication is that species having such tissues may have developed under arid conditions, inasmuch as under such conditions there may be organized a greater amount of cellulose and a smaller amount of starch than when the environment is humid. Moreover, in such an intensely arid region as central Australia, for example, the great abundance of sclerenchyma in foliar organs constitutes an important item in the support of such a view.¹ It then is an interesting circumstance that many species of the more arid portions of southern Africa are poor in the structural feature referred to. Without going further into this phase of the general question in this place, it can be pointed out that although many of the species have developed along the alternative line, that is, they are able to organize mucilages, there appear to remain species, not annuals, in which the power of converting polysaccharides into anhydrides is not especially well marked. It is such forms, along with those that are succulent, with one or two exceptions, that have been omitted *per force* in the present study of foliar structures.

A glance at the sketch of the more important or more striking features of the foliar structures, as given in the preceding section, will show relatively little uniformity in structural relations, although some important relations will appear. It will be seen that by no means all of the features are to be traced to the probable immediate influence of an arid environment, or at least the relation must be said

¹ Plant habits and habitats in the arid portions of South Australia. W. A. Cannon. Publication No. 308, Carnegie Inst. Wash., 1921, pp. 32 and 136.

to be obscure. At the same time it is borne in mind that here a single plant organ is dealt with, and not the root and shoot with the constituent organs; consequently judgment must be made with caution. However, certain deductions can be made which may be of interest, even with the limitations just implied.

In comparative studies on plant anatomy, from a physiological point of view, when an attempt is made to account if possible for peculiarities in structure, it is recognized that two different and important groups of forces are to be considered. These relate to the influence of heredity and to that of the immediate environment. In studies on desert plants the latter has often been stressed, doubtless owing to the spectacular association of perennials with conditions of little rain, when, especially to the physiologist, possibly little accustomed to such an environment, survival appears to be little less than miraculous. In such forms, as well as in those having more favorable moisture conditions, it is axiomatic that some consideration should be paid to influences outside of and apart from that of the immediate environment as well as to the latter. It is clearly impracticable to make direct comparison with ancestral forms, but it is not impossible to compare the structure of whatever species desirable with that of other members of the family which may be living under less arid conditions for the purpose of drawing conclusions as to morphological adjustments which may have been occasioned by such environment. Even so, and as will occur to every one, there will be lacunæ difficult or impossible to bridge, which may make conclusions tentative and subject to revision. However, possible suggestions, taken as such, may be worth while as a means of throwing some light on the directions of morphological adjustments, if in no other way.

EPIDERMIS.

The epidermal cells of the plants examined vary greatly in form. Thus some are squat and others are much elongated in a direction at right angles to the leaf-surface. The most striking of the epidermal cells observed were the vesicular ones of *Galenia africana*, which constitute a trichomelike covering of the leaf. The epidermal cells vary greatly also in size. This can be seen by an examination of the figures for *Aloe*, *Asparagus*, *Cadaba*, *Cussonia*, *Eriocephalus*, *Galenia*, *Protea*, and *Stachys*, all of which are drawn to the same magnification. In the case of *Grewia cana*, the epidermal cells of the two sides of one and the same leaf are of unequal size. Thus the area of a dorsal epidermal cell, in section, may be 7.6 times that of a ventral epidermal cell directly opposite, and the extreme difference in size of cells of the two surfaces is much greater than this. Thus, there is little uniformity among these xerophytes as regards the cell characters above referred to.

Possibly the most striking single anatomical character of foliar organs common to perennials of an arid region is the possession of a heavy outer epidermal wall. This feature seems to hold in all instances, except only in such species as have a permanent cover of trichomes. In such case, as in *Stachys* sp., the outer wall of the epidermis is thin. Where, also, a portion of the leaf only bears trichomes, as in *Grewia* and *Stæbe*, the exposed portion has a heavy outer wall, but in the protected part the outer wall is thin. That the exposed outer wall of xerophytic perennials should be heavy is not difficult to understand when it is recalled that such portions of the plant most intimately connected with the arid environment are most subject to drying, and that under such conditions anhydrides are formed, as mentioned at the beginning of the present section.

The general occurrence of a heavy outer epidermal wall in xerophytes, with the exceptions noted where the epidermal cells are not immediately in contact with the drying atmosphere, is therefore a characteristic of plants of this class. So far as the inner epidermal wall and the lateral walls are concerned, however, no such uniformity exists. The lateral walls appear to be variable in at least two directions, namely, as regards thickness and as regards the quality of being curved, undulating, or plane. Solereder states that the margins of epidermal cells of species of dry habitats are straight, while analogous cell-walls of species from moist habitats are wavy.¹ But the case is apparently not so simple as this. In mesophytic dicotyls the lateral walls are commonly straight on the dorsal leaf-surface and wavy on the ventral surface, and waviness culminates in mesophytic species. But in xerophytic and hydrophytic dicotyls and generally in monocotyls the side-walls are usually straight.² But the species used in connection with the present paper were not studied in this particular. So far as the thickness of the inner and the lateral epidermal walls are concerned, especially the latter, there is probably much variation, possibly within the species, certainly as between different species, and there is possibly no clear concordance between thickness and the character of the environment. The extreme in the formation of thick lateral walls appears in *Eriocephalus* sp., in which, mainly because of the extreme thickness of these walls, the cell lumen is nearly or entirely obliterated. A similar condition appears to obtain in the ventral epidermal cells of *Stæbe*. As regards the increase in thickness of the lateral walls, it is perhaps easier to explain why they should be greatly thickened in an arid habitat than that they should be subject to drying conditions and still not always suffer the fate of the outer wall.

¹ *L. c.* p. 905.

² A textbook of botany. Vol. 2, Ecology. Coulter, Barnes, and Cowles, p. 571. See, also, Haberlandt, *Physiologische Pflanzenanatomie*, Leipzig, 1904, p. 104.

Another noteworthy feature of the species studied is the general cuticularization of all or a portion of the outer wall. The deposition of cutin is closely associated with the transpiratory activity of the leaf and is not limited to xerophytes. Cutinization is less marked on the under surface of the leaf and in stomatal pits, and also is less in plants growing in protected situations than in situations that are exposed.¹ So far as was observed, the deposition of cutin is mainly, usually exclusively, in the outer epidermal wall, and not in the side-walls or the inner wall. As an exception, however, to the last remark it was seen that the lateral epidermal walls in *Cussonia spicata* give the same reaction with chloriodide of zinc as the outer wall, and are probably cuticularized. As regards the stomatal pores, the lining walls up to the guard-cells, and including the outer walls of the latter, may be cuticularized. The heaviest deposition of cutin was seen in the outer epidermal wall in *Asparagus striatus* and in *Cussonia spicata*, in which the unmodified cellulose constitutes only a thin inner lining of the wall.

Yet another feature of the epidermis which should be mentioned is the occasional presence of a waxy cover on the cuticle. It was observed in *Galenia africana*, *Royena pallens*, and *Asclepias filiformis* (?) as a granular coat. As in the case of the formation of cutin, that of wax is not confined to xerophytes, although it is best developed in plants of this class. Unlike cutin, wax is heaviest on the under surface of leaves, but, like cutin, it is best developed under conditions of excessive transpiration. The point is made that the formation of wax, or resin, as an outer coating of the foliar organs of the species studied can not be said to be the usual occurrence, but, on the other hand, it appears to be fairly rare. This is rather surprising from the known fact that a waxy covering of the leaves cuts down the loss of water very considerably. Thus, Haberlandt² cites the results of experiments which indicate that leaves with the natural coating of wax carefully removed evaporate from 1.1 to 1.5 times more water in unit time and for unit leaf area than the same leaves with the wax in place.

Although not observed in the species here considered, it is known that the cuticularized portion of the outer epidermal wall, in the leaves of *Mesembryanthemum* sp.³ and of *Welwitschia mirabilis*,⁴ may contain minute crystals of calcium oxalate. Larger crystals of different form are present, often in great amount, in different parts of the leaves in most of the species examined. The inclusion of inorganic substances, including calcium oxalate, in old cell-membranes is apparently not restricted to the epidermis or to species which inhabit arid habitats.

In no species was the inner epidermal wall found to be at all com-

¹ A Textbook of Botany. Vol. 2, Ecology. Coulter, Barnes, and Cowles, p. 569.

² Physiologische Pflanzenanatomie, G. Haberlandt, Leipzig, 1904, p. 99.

³ Solereder, l. c., p. 470.

⁴ The anatomy and morphology of the leaves and inflorescences of *Welwitschia mirabilis*, M. G. Sykes. Phil. Trans. Roy. Soc. London, Ser. B., vol. 201, p. 181. 1910.

parable to the outer wall in thickness, and usually it is relatively or actually thin. Only in the case of *Cussonia spicata* can the inner wall of the outer cell-layer be said to be heavy, and in this instance the comparison falls down, for the reason that the epidermis of *Cussonia* is several cells in thickness. However, the physiological inner epidermal wall, which lies several cells beneath the outer epidermal layer, is, in this species, fairly heavy, although pores do not appear to be present. The inner wall is apparently never impregnated with cutin, which would hinder the free passage of water, and material in solution, to or from the epidermal cell. The inner wall of all species examined in this particular gave the cellulose reaction with suitable reagents, and no indications were seen of its being converted into mucilages, although mucilaginous inner epidermal walls are known in species of the Liliaceæ, Tiliaceæ, and Leguminosæ.

In *Cussonia spicata* and in *Gymnosporia buxifolia* the epidermis, dorsal in the species first named, consists of more than one cell-layer.¹ In *Cussonia* the hypoderm is several cells thickness and constitutes an important portion of the mechanical tissues of the leaf, but in *Gymnosporia* it is only one cell in depth. In the latter species the hypoderm may contain crystals of calcium oxalate, although many of the cells have heavy walls and are provided with pits.

Solereder (*l. c.*, p. 910) gives a list of families of which some species may have a hypoderm. Among these, and in addition to the Tiliaceæ, to which *Gymnosporia* belongs, and the Araliaceæ, of which *Cussonia* is a member, and which are represented by species whose structure is mentioned in the present paper, are the following: Apocynaceæ, Asclepiadaceæ, Capparidaceæ, Compositæ, Leguminosæ, Protaceæ, and Scrophulariaceæ. In the two species only, however, as mentioned above, was hypoderm found.

STOMATA.

The distribution of the stomata on the leaf and the position of the guard-cells with relation to the general level of the leaf-surface are various and have different apparent correlations. But among other variable features, more or less related to that last named, may be mentioned the development of the vestibule, as well as that, in some instances, of an outer vestibule, the stomatal pit, also. It will be seen that the presence of certain of these features is in apparent relation to the fact of an arid environment, although the relation may not be immediate and direct.

The distribution of the stomata as between the dorsal and ventral surfaces follows in general the symmetry of the leaf-structure. That is, in dorsi-ventral leaves the stomata are confined to the ventral

¹ In this account no distinction is made between hypoderm and multicellular epidermis, although the two have unlike origins. The physiological rôle played by them may be similar.

surface, otherwise they are on both surfaces. In the case of *Stæbe* sp., however, where the chlorenchyma of the ventral side is palisade-like, and hence in which the symmetry is modified dorsi-ventral, the stomata are nevertheless confined to the ventral surface.

The relative number of stomata was observed in one case, namely, *Cotyledon paniculata*, where comparison was made with the number in a cultivated variety of the sunflower. In this instance there was approximately twice as many stomata per unit area in the sunflower leaf as in that of the *Cotyledon*.

The guard-cells of stomata of the species examined lie in some below the general surface of the leaf, in other species somewhat above, and in other species they are fairly flush with the leaf-surface. In such stomata as are more or less deeply placed, the depth of the guard-cells is in large part dependent on the thickness of the outer epidermal wall, although there are exceptions to this statement. Thus in *Cadaba juncea* it is the depth of the epidermis as a whole that determines that of the stomata, and a similar condition obtains in *Euryops lateriflorus*, as well as in *Protea neriifolia*. It was found, however, in many species that the guard-cells were not deeply placed, although the outer epidermal wall might be fairly heavy. As examples of the last, *Antizoma capensis*, *Aptosimum indivisum*, and *Carissa ferox* can be mentioned. In *Stachys* sp. and *Stæbe* sp. the guard-cells project somewhat above the general level of the leaf. In the species last named there is a heavy and permanent cover of trichomes on the portion of the leaf where the stomata are situated.

The outer guard-cell ridges, which delimit the outer portion of the outer vestibule, are well developed in some species, as in *Aptosimum indivisum*, *Antizoma capensis*, and *Cadaba juncea*, and may be in others as well. They serve as a means of constricting the approach to the stoma and in many species constitute the only protection, of this sort, to it. In such, however, as have deeply placed stomata the very entrance to the stomatal pit, or chamber, may be constricted in such way and to such an extent as to make possible the delimiting of a second outer vestibule, as in *Euryops lateriflorus* and *Protea neriifolia*. The guard-cell ridges and the inner portion of the secondary vestibule are cuticularized.

TRICHOMES.

Trichomes were found in 12 of the 27 species whose leaves were studied, and may possibly be found in young leaves of others. In *Stachys*, trichomes cover the mature leaf and in *Stæbe* they are present on the ventral surface only and are persistent. But for the most of the species with trichomes the cover trichomes, at least, fall away in age. It can be rightly concluded, therefore, that, so far as the species referred to are concerned, the occurrence of trichomes is not a marked

characteristic or one that is particularly to be associated with an arid habitat. It should be remarked, also, that in few, if any, of the species studied was there found excessive development of glandular trichomes, or evidences of very active secretion on their part (but see *Rhus* sp. above). There was nothing, for example, at all comparable to the condition which was found in the genus *Eremophila* in southern Australia, and in *E. freelingii* in particular, where the exudation from the trichomes quite covered the glandular hairs themselves.¹

In *Eriocephalus* sp., the base of the cover trichomes is cuticularized, while the middle and the distal portions are unmodified cellulose, and this seems to be the condition of the trichomes in several other species as well.

The correlation of a covering of trichomes and a thin outer epidermal wall has been commented on in a preceding paragraph. (See also, *Euclea undulata* in this regard.)

MESOPHYLL.

The fundamental tissue of the leaves of the species examined varies in the direction and in the degree of development and apparently is somewhat less directly affected by the arid conditions of the environment than are the integumentary tissues. However this may be, there are trends in development which appear to have correlations with the more striking environmental factors which indicate possible degrees of "usefulness" if not of direct cause and effect; and certain of these can be mentioned in this summary of the main structural characteristics of the mesophyll.

Of the species examined, 18 were observed to have the same kind of chlorophyll-bearing cells on the two sides of the leaf, that is, they are isosymmetrical, 6 have well-defined dorsi-ventral structural symmetry, and in 3 the symmetry is intermediate. Where the structure is symmetrical, the chlorenchyma is of palisades, except in the case of succulents, as *Aloe variegata*, for example, where the outer layer of the mesophyll is neither cuboid nor palisade, but is somewhat elongated in a direction away from the surface of the leaf. It appears, therefore, that for the most part the chlorenchyma of the species studied is composed of cells whose longest axis is at right angles to the leaf-surface.

Although the material available for study was for the most part not in condition suitable for determining the point as satisfactorily as would be desired, it was observed, however, that the extent of the intercellular spaces of the chlorenchyma was exceedingly varied; and further, that in palisade chlorenchyma the intercellular spaces are relatively small, being smaller in well-developed than in poorly-developed or modified palisade tissue; and they are best developed in

¹ Plant habits and habitats in the more arid portions of South Australia, *q. v.*, p. 128.

spongy parenchyma, that is, in species having dorsi-ventral structural symmetry of the leaves. As to a possible correlation of this condition with the aridity of the habitat, and there is clearly correlation, there are striking exceptions. For example, *Asclepias filiformis* (?) occurs in the habitat of *Welwitschia mirabilis*, in the Namib Desert. The structure of the leaf is dorsi-ventral. But *Protea neriifolia* is to be found when the rain is very considerable, even if there are fairly long periods without rain, and still the two sides of the leaf are apparently alike in structure. Further than this, species having cuboid chlorenchyma, and those with chlorenchyma which is of palisades, may grow in close proximity. But, it is to be remarked, the first of these may be succulent and the last, apparently with no exception, is sclerophyllous. The well-marked difference in metabolic processes, as between the two classes of plants, very evidently overcomes possible direct morphogenic effect of light on the chlorophyll-bearing cells.

Reactions with the use of chloroiodide of zinc indicate that the cuboid chlorenchyma of *Aloe variegata* contains mucilages. In many sclerophyllous species calcium oxalate in crystals is to be found in the chlorenchyma, or other cells, of the mesophyll; and, finally, in the idioblasts of *Cadaba juncea*, which occur to a certain extent in the chlorenchyma, there may be mucrosin (?).

Heavy-walled tissues, either fibrous or isodiametric, are often marked characteristics of xerophytes. Such tissues were found to be prominently developed in many perennials of South Australia.¹ Under such conditions the amount of living tissue is very markedly reduced, and with this as a result the water requirement, in proportion to the mass of the plant, becomes small.

The mechanical tissue is commonly importantly developed in relation to the fibro-vascular bundles, where it occurs dorsally and ventrally, sometimes (as in *Euclea undulata*) reaching nearly to the epidermis. It is especially marked in association with the midrib, but a few strands of fibers are often to be found with the smaller strands of conductive tissue. In *Asparagus striatus* leaves (?) the supporting tissue constitutes a ring which separates the chlorenchyma from the more deeply lying fundamental and conductive tissues. Of the species studied in this regard, 6 were not noted to have sclerenchymatous elements of the types referred to, but in 16 species supporting tissue, fibrous, was present.

CONDUCTIVE TISSUES.

Although the conductive tissues were not especially studied, it was evident, from casual inspection, that those of the foliar organs vary in a broad way and in a manner characteristic of the type of plant or

¹ Plants and plant habitats in the more arid portions of South Australia. W. A. Cannon, *q. v.*, p. 136.

of leaf. Thus it was noted that the mass of tissue of this character, as related to the mass of the chlorenchyma, was very meager in *Aloe variegata* and *Cotyledon paniculata*, but that it was relatively abundant in all sclerophylls.

NOTES ON THE ORIGIN OF FOLIAR STRUCTURES.

A cursory glance over the most striking structural features of the leaves of the xerophytes mentioned in this paper leads to the inevitable conclusion that, at least as regards the species studied, very diverse morphological roads have been followed during the long processes of adjustment to their respective environments, a leading characteristic of each of which is the greater or smaller degree of aridity. But it is also recognized, as mentioned in an earlier paragraph, that the foliar organs are only a portion of the "plant," and that to have a satisfactory conception of the morphological relation of the plant to the environment it is also necessary to take into consideration the nature of the development of the root as well as of the shoot in its entirety, including the leaves; but in the present study it is not possible to do this. The writer, therefore, has been obliged to be content with comparing the structure of the leaves of different species belonging for the most part to unlike families. Conclusions based on such meager foundation are necessarily tentative, but, nevertheless, it is believed that they are sufficiently interesting and suggestive to be worth undertaking. In order to estimate the possible influence on leaf-structure of family characteristics, and indirectly of inherited qualities, a running summary of the leading morphological features of the leaves of the families here represented will be given in the following few pages, together with something of their geographical distribution, especially as regards southern Africa, and a short recapitulation of specific structures as given somewhat in detail above.¹ The immediate result of such a comparison should place the direct effect of the environment on the morphology, especially the inner morphology, of the leaf in all the sharper relief.

PROTACEÆ.

The Protaceæ, although occurring rarely in South America and New Zealand, are especially abundant in southern Africa and Australia.

¹ Authorities generally available were used in determining the general distribution of the families, and these were supplemented by recent publications by South African writers, among which are the following: The flora of Natal and Zululand, J. W. Bews, Pietermaritzburg, 1921; Some general principles of plant distribution as illustrated by the South African flora, J. W. Bews, Ann. Bot., vol. 35, 1921; Plant succession and plant distribution in South Africa, J. W. Bews, Ann. Bot., vol. 34, 1920; Phanerogamic flora of the divisions of Uitenhage and Port Elizabeth, S. Schonland, Bot. Sur. So. Africa, Mem. No. 1, 1919; Das Kapland, R. Marloth, 1908; The veld: Its resources and dangers, I. B. Pole Evans, So. Af. Jour. Science, vol. 17, 1920. The general account of the morphology of the families was taken for the most part from Anatomie der Dicotyledonen, H. Solereder, Stuttgart, 1899. Other authorities, however, were also referred to, but they are generally available and need not be given specifically.

There are 264 species in the Cape Province. A marked peculiarity of the African species, as opposed to those in Australia, is that whereas in the latter continent many of the family are to be found in arid regions, in southern Africa all of the species are apparently restricted to habitats which are humid or only periodically dry.

The anatomical characters of the large family consisting of herbs, shrubs, and trees, are various, but the following respecting the leaf may be mentioned: The structure may be isosymmetrical or dorsi-ventral. Sclerenchyma may occur in the mesophyll, and there may be hypoderm. The stomata may be superficial or deeply placed. The leaves are mostly reduced in size and leathery in texture.

Protea neriifolia, the structure of which is outlined in an earlier section, has palisade chlorenchyma, a heavy outer epidermal, and fairly deeply sunken stomata. Sclerenchyma is present in connection with the conductive tissue. The relatively small development of sclerenchyma, however, is a marked contrast to the condition characteristic of such a species as *Hakea leucoptera*, for example, of arid South Australia.¹

MENISPERMACEÆ.

The Menispermaceæ is largely tropical and is represented in southern Africa by about 7 species, of which 6 occur in Natal-Zululand district and 2, one being common to the two districts, in Uitenhage-Port Elizabeth. The plants are undershrubs, shrubs, and climbers.

The leaf is generally dorsi-ventral and isosymmetrical in structure, whereby the chlorenchyma in palisades is rarely found. Mucilaginous strata may be organized. Sclerenchyma may be present in the mesophyll. One-celled or two-celled cover trichomes and multicellular secretion hairs occur in some species, and also hydathodes, among other structural features.

Short palisades were found on both sides of the leaf in *Antizoma capensis*, and a heavy outer epidermal wall, which, together with the relatively small leaflets, are the main xerophytic characters. These, especially the former, are apparently unusual in the family.

AIZOACEÆ.

The Aizoaceæ are succulents which occur chiefly in southern Africa, although a few species are to be found in the Mediterranean region, Australia, and America.

Of the family, *Galenia africana*, one of the species studied in this paper, and numerous species of the genus *Mesembryanthemum*, are abundant in the Karroos, including the Upper and Lower Karroo. Succulents, including many species of the genus last named, are

¹ Plant habits and habitats in the arid portions of South Australia. W. A. Cannon. Carnegie Inst. Wash. Pub. No. 308, 1921, p. 120.

dominant in the southern portion of the Karroos. The diversity of forms is most marked.

Among the most striking anatomical features of the family are the following: Most highly characteristic is the (frequent) great differentiation of the epidermis, in which the development of vesicular cells with water-storage capacity is a feature. The leaf-structure is isosymmetrical as to the mesophyll, in which the entire mesophyll *may* be palisades or only the subepidermal layers (or modified palisades). There may be a wax covering to the epidermis (*Mesembryanthemum* sp.) or trichomes by which the rate of water-loss may be lowered. In a few species of *Mesembryanthemum* (*M. glaucum*, etc.) tannin ducts are to be found, one or two cell-layers under the epidermis. Calcium oxalate is present as crystals of various types, of which some are minute and occur in the membrane of the epidermis as determined first by Solms-Laubach.¹ Finally, it should be mentioned that the organization of mucilages is a characteristic of at least species of *Mesembryanthemum*.

Galenia africana conforms in the epidermal structures, in the character of the trichomes, and in the presence of calcium oxalate, to these family features, but whether in the metabolic processes pentosans, or mucilages, are formed by the species has not been determined. *Galenia* is not a true succulent. The transpiration surface is greatly reduced and, as appears in another connection, the form of root-system is typical of sclerophytes rather than of species with water-balance. It is not clear, therefore, whether the species exhibits direct adjustment to its environment, so far as its morphology shows this, beyond the reduction in the leaf-surface.

CAPPARIDACEÆ.

The Capparidaceæ are herbs, shrubs, climbers, and trees of the tropics and subtropics. There are over 20 species in southern Africa, of which 17 occur in Natal and 6 in the Port Elizabeth-Uitenhage district, 3 of these being in both regions.

The anatomical characters of the leaves of the family are extremely varied and need not be set forth in this place (cf. Solereder, p. 78). Certain features which appear to run through the family may, however, be referred to. For instance, sclerenchyma of various types is present in the mesophyll. Calcium oxalate mostly occurs as spherical masses or small prismatic crystals. Two-armed or two-branched unicellular trichomes occur in some *Capparis* species, but the kinds of cover trichomes are "endless."

In the course of adjustment to arid conditions, *Cadaba juncea*, the representative of the family studied, has undergone a marked reduc-

¹ Ueber einige geformte Vorkommnisse oxalsäuren Kalkes in Lebenden Zellmembranen. Bot. Zeit., 1871.

tion in the foliar transpiration surface, and has developed tissues with heavy walls, namely, outer epidermal wall and both fibrous and tracheid-like sclerenchyma. The stomata of green branches are deeply placed and the outer vestibule well developed. The palisade type of chlorenchyma is present.

TILIACEÆ.

This great tropical genus is represented in southern Africa by 19 species or less.

Mucilaginous cells occur in the epidermis in some species of one section of the family. The structure of the leaf may be isosymmetrical, although for most of the species it is dorsi-ventral. Both cover and secretion hairs occur. For other details the reader is referred to Solereder, page 176.

The leaf of *Grewia cana*, as representing the Tiliaceæ, was found to have a heavy covering of trichomes. The epidermis is not heavy and the outer wall is thin. Although in the section to which the genus belongs mucilage cells are not reported for the epidermis, the reaction with chloriodide of zinc seems to show that the epidermal cells do in fact contain mucilage to a certain extent, even if there may be no especial mucilaginous epidermal cells.

ANACARDIACEÆ.

The Anacardiaceæ occur chiefly in warm countries. Of the family, the genus *Rhus* is largely represented in southern Africa, and extends through tropical Africa, northern Africa, the Mediterranean region, Arabia, India, the Himalayas, China, North America, and Mexico, according to Bews, who gives the following information regarding the distribution of the genus in South Africa:¹

“When we look at the present-day distribution of the species of *Rhus* in South Africa, we find certain of them * * * very widespread, as pioneer species in the xerosere. Other * * * occur along the streams and are important in the hydrosere, or * * * occur on the coast sand-dunes in the psammosere. As succession advances, we find species of *Rhus* * * * dominant in climax vegetation on the dry doloritic Karroo kopjes. * * * In more mesophytic forest areas we find various steps in the adaptation to more favorable conditions in a large series of forms till we reach such large forest-trees as the red currant (*Rh. lævigata*), which grows fifty to eighty feet high, and two to four feet in stem diameter. *Rhus* also shows adaptation to purely grassland conditions.”

Two species of *Rhus* were studied in connection with leaf-structure, of which one, *Rhus viminalis*, is found in or along the streamways of the Karroo, usually dry, and the other, *Rhus* sp., occurs on the top of kopjes, at least in the western part of the Karroo.

¹ Some general principles of plant distribution, etc., l. c., p. 19.

Among the leading structural features of the leaf of the family are the following: Resin channels are present and simple one-celled trichomes and glandular trichomes of the greatest variety of form, which in certain species may secrete a lacquer covering to the leaf. Sclerenchyma is given as a character of the (primary) cortex, but is not included by Solereder among the anatomical features of the leaf.

Inasmuch as the leading points of foliar structure for the species of *Rhus* studied has been given in an earlier paragraph, it will only be necessary in the present connection to call attention to the following: In both species examined the structure is dorsi-ventral, but the palisades are relatively much longer in *Rhus viminalis* than in *Rhus* sp. Sclerenchyma is developed in connection with the veins in both species, but is more pronounced in the former than in the latter. In neither species is the outer epidermal wall especially heavy. A heavy resinous (?) coating occurs on the dorsal surface of *Rhus* sp. This feature was not observed in *Rhus viminalis*.

CELASTRACEÆ.

The Celastraceæ is a rather small family of widely scattered species of shrubs, lianes, and trees, being found in the tropics and subtropics and temperate zones of both hemispheres, and in all continents, including Australia. Of the family about 47 species occur in southern Africa, approximately one-half of which are in the Natal region.

Among the structural features which occur in the family are the following: Mucilaginous epidermal walls, calcium oxalate as spherical crystal masses or single crystals; hypoderm; resin cells in epidermis and mesophyll; sclerenchyma not given for leaf, but present as fibers in cortex of stem.

In *Gymnosporia buxifolia* leaf the outer epidermal wall is heavy, the guard-cells of the stomata are somewhat raised above the general leaf-surface, a hypoderm is present, and sclerenchyma occurs in association with the conductive tissue. The marked development of spines, morphologically branches, and reduction in size of the leaves, are further indications of an adjustment to arid environment. It is perhaps worthy of note that the chlorenchyma is not of true palisades and such are not reported by Solereder for other species of the family.

ARALIACEÆ.

The Araliaceæ are chiefly tropical. About 7 species are found in southern Africa, all in Natal, and but 2 in the Uitenhage-Port Elizabeth district.

The anatomical features of the leaves are various and include hypoderm on the dorsal side, secretory ducts, extremely variable glandular and cover trichomes, secreting-cells of calcium oxalate, dorsi-ventral symmetry, etc.

In *Cussonia spicata* the hypoderm is the most striking anatomical feature, although the outer epidermal walls of both surfaces are fairly well developed. It should be noted that Solereder (*l. c.*, p. 483) cites 22 species in which a hypodermal development occurs. Of these, only 2 species are given by Marloth (Das Kapland) for South Africa, both of which are of the genus *Cussonia*. Secretory ducts occur in connection with the conductive tissue. There is little sclerenchyma. There appears, therefore, to be little in the foliar tissues to suggest structural development in relation or adjustment to a severely arid environment, which accords with the known distribution of the species in which such conditions are apparently avoided.

LEGUMINOSÆ.

This large family is well represented in southern Africa, 283 species being reported from the Natal-Zululand district and 149 from the Uitenhage-Port Elizabeth district. Species of the Leguminosæ are to be found very generally distributed throughout the subcontinent. Of the family, *Sutherlandia frutescens* is given by Bews as an example of an isolated species with no obvious connections,¹ but apparently very widely distributed, and *Bauhinia marlothii* is of small genus and the species may be limited to the arid Namaqualand district. The former is of the subfamily Papillionatæ and the latter of the Cæsalpinæ.

PAPILLIONATÆ.

The anatomical features of the subfamily are so varied that no attempt can be made in this place to summarize them. However, a few salient characters can be pointed out, as follows: Among the features common to the subfamily are the failure of spherical crystals (aggregates), and that of common unicellular trichomes, and, of positive characters, the occurrence of rod-shaped crystals and of elongated, tubular cells containing tannin or albuminous substances. Thus the want of common structural features, with the correlation, great variation in structure, are noteworthy characteristics. For details the reader is referred to the account by Solereder and the references there cited.

It will be seen by referring to the sketch of some of the leading anatomical features of the leaves of *Sutherlandia frutescens*, as given in an earlier section, that the development of palisades on both sides of the leaf and the presence of a heavy outer epidermal wall, bespeak the expected structural adjustment to an arid environment, but the apparent absence of sclerenchyma may be of phylogenetic significance. Not enough is known, however, regarding the leaf anatomy, either of the species in question or of those most nearly related to it, to consider the subject further at the present time.

¹ Some general principles of plant distribution as illustrated by the South African flora. *Ann. Bot.*, vol. 35, p. 19, 1921.

CÆSALPINÆ.

There are few anatomical characters of the leaf held in common by the subfamily Cæsalpinæ, but among such are the occurrence of calcium-oxalate crystals in spherical masses and the formation of simple, unicellular trichomes, although the last-mentioned feature is not without exceptions. For greater detail the reader is again referred to the summary by Solereder (p. 319), but the following points can be mentioned: The epidermis is mostly of one cell-layer, the chlorenchyma of some species is of palisades, in some species the epidermis is subpapillose and in other papillose. The stomata are mostly on the ventral surface, and the guard-cells usually on a level with the leaf-surface. Sclerenchyma of various types may be present.

As to the foliar structure of *Bauhinia marlothii*, which has already been outlined, it is sufficient for the present purpose to point out that the fairly large leaflets have chlorenchyma of palisades on both faces, that trichomes are wanting, as also is sclerenchyma, and that the epidermal cells in age become papillose, or at least subpapillose. In this case the outer epidermal wall is thin, and, as occurs when there is a heavy cover of trichomes, the stomata are superficially situated.

CRASSULACEÆ.

The Crassulaceæ, which are herbs or undershrubs, are to be found in warm temperate regions, about one-half being in southern Africa. But some occur in Australia, southern Asia, and central subtropical America, the Mediterranean region, etc. There are about 108 species in southern Africa, about one-half of which occur in Natal and Zululand. Of the genus *Crassula*, 34 species have been reported from the Central Provinces, the Karroos, and 14 from the arid region northwest of the latter.

The following are some of the leading structural characteristics of the leaves or chlorophyll-bearing organs of the family. True palisade cells are seldom formed. Stomata usually are on both leaf-surfaces. A covering of trichomes is unusual. Calcium oxalate may be formed as single crystals, spherical masses, or fine crystals; in the latter event they may either be in the lumen of the cells or embedded in the walls. A waxy covering of the epidermis sometimes occurs. But the most striking feature of the family as a whole is the presence of mucilages and the general succulent habit, extending to the leaves, which, in some species, are strongly developed, in which case the forms are so-called leaf succulents.

The leaf of *Cotyledon paniculata*, which, although fleshy, is deciduous, conforms in the main features of its structure to the general structural relations of the family. These have already been sketched. It is sufficient to point out here that heavy-walled supporting tissue is absent and that the leaf is highly mucilaginous. Associated possibly

with the fact that the leaf is fugacious, the outer "protective" covering and structural arrangements of whatever kind of the leaf, do not appear to be suitable to withstand successfully severe dryness of the atmosphere. The species is a stem succulent.

LABIATÆ.

The large family of the Labiatae is largely found in the Northern Hemisphere, and especially in dry and sunny situations which appear to be favorable for the formation of the ethereal oils characteristic of it. In southern Africa it is largely represented in the Natal-Zululand districts, in which 98 species occur. In the region about Uitenhage and Port Elizabeth are 42 species, of which 15 are common to the two floral districts. So far as concerns the genus *Stachys*, which has been examined in the present study, 21 species are in the region first named and 9 are in the one farther southwest; 4 species are common to the two. The Labiatae do not appear to be found to any extent, if at all, in the semi-desertic regions of the subcontinent.

In a family so large, consisting of over 2,700 species, the foliar structures are necessarily various, even if the family as a whole is one of the most natural plant groups. For greater details the reader is referred to Solereder (p. 718) and to the authors there cited. It will be sufficient for the immediate purposes to point to the following structural features: Secretory trichomes, from which the ethereal oils are derived, are of variable structure, as also are the cover hairs. Both may be extensively developed and form special characteristics. Hypoderm is present in certain species, and resiniferous cells as well.

So far as regards the structure of the leaf of *Stachys* sp., an outline of which is given above, it need only be mentioned that there are no apparent structural features which point to the immediate influence of an arid environment, unless it is the formation of a heavy covering of trichomes, and this, as will be seen from the above sketch of family structural characteristics, may be regarded as being only a possible accentuation of tendencies already possessed by other species of the family.

SCROPHULARIACEÆ.

The Scrophulariaceæ is a cosmopolitan family occurring mostly in temperate regions. According to Bews, there are 21 genera, widely scattered over South Africa, of which 3 are in the Kalahari region. "Most of the genera afford examples of widespread species giving rise to rare endemics."¹

Solereder gives an extensive list of structural peculiarities of the leaf, to which the reader is referred. These include great variety of cover and secretion hairs; calcium oxalate seldom occurs and then in

¹ Some general principles of plant distribution as illustrated by the South African flora. J. W. Bews. Ann. Bot., vol. 37, p. 24, 1921.

small crystals, rarely in large crystals or in crystal aggregates. Crystals of carotin and protein crystals frequently are to be found in the mesophyll. The leaf-structure is isosymmetrical or dorsi-ventral. In desert species the epidermal cells have heavy walls and carry tannin.

So far as concerns the structure of *Aptosium indivisum*, which was studied and the leaf-structure of which was sketched in an earlier paragraph, it is sufficient to remark that the leading features of the structure are the very heavy outer epidermal wall and the palisade chlorenchyma, and are very evidently adjustments to the environment.

ASCLEPIADACEÆ.

The Asclepiadaceæ, which is mainly tropical, is largely represented in southern Africa and chiefly in the Zululand-Natal district, where 156 are reported; 65 species occur in the Uitenhage-Port Elizabeth district.

The anatomical features of the family, as well as the gross morphology, are strongly diverse. It will be sufficient in this place to point to the following relative to the leaves: The structure may be dorsi-ventral, or the mesophyll may be alike on the two sides. Hypoderm may be present. Sclerenchymatous fibers as well as latex tubes run irregularly in the mesophyll. Some species have succulent leaves. In species from the arid regions the cuticula is highly developed, and there is secretion of wax. Many species are stem succulents, which connotes the organization of mucilages, and hence the possession of a distinct type of metabolism.

Asclepias filiformis (?), a sclerophyllous species, as has been described in the preceding section, possesses certain structural features which conform to those known to be characteristic of the family as a whole and which need not be repeated here; but in certain regards, also, it is evident that there is a response to an arid environment, as evidenced by the character of the tissues as a whole. Thus, there is a relatively large development of cell-walls, and especially of the outer epidermal wall, and a fairly large proportion of non-living material.

APOCYNACEÆ.

The Apocynaceæ are chiefly tropical and are comparatively rare in extra-tropical hot and temperate countries. There are about 22 species in southern Africa, of which 18 are listed as occurring in the Zululand-Natal district; 1 species occurs in the Karroo region.

The structure of the leaf of members of this family as outlined by Solereder, to whom the reader is referred, is exceedingly varied. The leaves may be dorsi-ventral, or the structure may be similar on both leaf-surfaces. There may be hypoderm, and cover hairs of various forms are to be found. The stomata are of different types.

The cell-walls in the spongy tissue may be mucilaginous, and, finally, there may be palisade sclerenchyma.

As to the special structural features of *Carissa*, which are mentioned more fully above, it need only be pointed out that there is a marked reduction of the transpiration surface, a heavy outer epidermal wall is formed, and sclerenchyma occurs in association with the conductive tissue. It is not impossible that all of the leading morphological characters of the species, except possibly the heavy outer epidermal wall and the reduced surface, can be duplicated in other members of the family which occur in less arid habitats.

EBENACEÆ.

Species of Ebenaceæ occur in tropical and subtropical regions of Asia, South Africa, Australia, and America; they are rare in the Mediterranean region. In southern Africa the family is largely represented in the south and southeast, but species of *Royena* and *Euclea* occur in the arid central province, the Karroos, as well.

The structure of the leaf is generally dorsi-ventral. Hypoderm is formed in some species. Sclereids are sometimes to be found, but seldom in the mesophyll. Cover hairs, of simple structure, are characteristic, but two-armed trichomes and glandular trichomes are also formed. Mucilages are not organized.

Euclea undulata and *Royena pallens* were examined. Both species agree in having trichomes, especially in the young leaf. Where they persist the outer epidermal wall is light, otherwise it is heavy. The stomata are not sunken. In *Euclea* the structural symmetry is dorsi-ventral and sclerenchyma occurs with the conductive tissue. In *Royena* the chlorenchyma is palisade and of modified palisade, with the effect that the symmetry is modified accordingly. There appears to be no sclerenchyma in this species.

Apparently neither of the species mentioned has an extreme type of xerophytic leaf-structure and also apparently neither occurs in the most arid situations.

COMPOSITÆ.

In South Africa over 40 genera of the Compositæ are of general distribution, over 40 genera mainly in the southwest, a small group mainly central, about 20 genera from the Transvaal and Natal along the coast of the south, and a few with restricted distribution. Of the genera whose leaf anatomy is sketched in this paper, *Pteronia* is strongly represented in the Karroo provinces and in the arid region to the northwest, but apparently is not reported from Natal, but occurs in the Port Elizabeth district. *Euryops* is also represented in these two arid regions, but occurs also in Natal, as well as in Port Elizabeth district, and the same can be said of *Pentzia*.

Owing to the great number of species of this family and the complexity of the life-forms, and that of the structure of the foliar organs, it is not practicable in this place to present an outline of the anatomical characteristics, particularly of those representatives of the family which live in the more humid region of the subcontinent, of which the anatomy may not have been worked out. Reference to the outline of the structure of the leaves of the genera represented in the study in a foregoing section will give some idea of the structural adjustment to such conditions of aridity as obtain where they were observed in the field. It will be seen that there are in general such structural features as may be expected under such conditions, including a heavily developed outer epidermal wall, which may lead almost to the total obliteration of the lumen of the cells, and generally these features include marked development of sclerenchyma as well. There is also in certain of the species, and particularly when young, trichomes of various kinds, and in certain of them secretory ducts. Such characters, with a reduction in the transpiration surface, possibly would separate these species from the related species of the more humid regions, whatever the structure otherwise of the latter might be. But as to the more exact possible derivation of structures in these xerophytes, it seems at the present impossible to speak.

SOME CONCLUSIONS.

In considering the relation and possible origin of the foliar structures dealt with in this section, it is desirable to call to the attention the following points, which, for the sake of clearness and brevity, will be stated didactically:

(1) As the summaries of the distribution of the families indicate, it is apparent that the family of each species used is also in part to be found under favorable conditions, so far as the rainfall is concerned. This is not an unusual condition, since, according to Bews,¹ "the examples of xerophytic shrubby species being closely allied to the mesophytic forest species are * * * very numerous."

(2) The brief statements of the main foliar structural features of the families compared to the summaries of the same characteristics for each species indicate that often, if possibly not always, the definite family characters may be clearly recognized in the xerophytic relative. The characteristic structures of the xerophilous species are, thus, in part a modification of family structures by reason of which, at least as indicated by the morphology of the leaves alone, survival is accomplished.

(3) The list at top of page 21 partially summarizes the observed xerophytic structures and suggests the family ones of which they may be a modification.

¹Some general principles of plant distribution as illustrated by the South African flora, *Ann. Bot.*, vol. 35, p. 31, 1921.

MESOPHYTES.

Leaves various, often of large size and relatively thin.

Trichomes often present, at least in young leaves; cover and glandular trichomes, the latter of which may secrete various substances, including those which are resinous, and ethereal oils as well.

Outer thin epidermal wall, lightly cuticularized, may be covered lightly with wax of epidermal origin.

Stomata, superficially placed, provided with outer vestibule ridge. Portion of guard-cell walls may be cuticularized.

Structural symmetry usually dorsi-ventral. Chlorenchyma cuboid or palisade.

Sclerenchyma may be present; if so, usually in association with fibro-vascular bundles, but not strongly developed.

Metabolism leads to the formation of a relatively small amount of cell-wall material, and but little material that is mucilaginous.

XEROPHYTES.¹

Leaves usually small, or wanting, and never thin, sometimes succulent.

Trichomes may be persistent. Cover trichomes may be associated with marked xerophytic type of epidermis. Glandular trichomes may secrete heavy outer waterproof coating of leaf, or may organize ethereal oils.

Outer epidermal wall may be very thick, may be heavily cuticularized, and may give rise to an outer cover of wax.

Stomata may be superficially or deeply placed; if the latter, the pit may be constricted at entrance as well as by other vestibule ridges. Portion of guard-cell walls may be cuticularized, and those of the pit as well.

Structure either isosymmetrical or dorsi-ventral. In the former chlorenchyma of palisades, or in succulents cuboid or modified palisades.

Sclerenchyma may be a marked structural feature; usually in connection with conductive tissue.

Under arid conditions the polysaccharides may be largely converted into anhydrides or wall material, or, in less arid conditions, into pentosans or mucilages (succulents).

¹ Unmodified or slightly modified family characteristics are not included in the list.

OBSERVATIONS ON THE FOLIAR TRANSPIRING
POWER IN WINTER AND SPRING.

The studies on the transpiring power of some perennials of southern Africa were carried out during the cool season, between the last of June and the last of October, on species in the Namib Desert, and especially in the Central Karroo.

The Stahl-Livingston cobalt-chloride method was used, with certain minor changes to adapt it to the conditions met in the field work. Thus, in order to dry the hygrometric paper, use was made of a folding photographic dark-room lantern having a metal top. The heat was obtained by the use of short candles, "night-light," which are contained in flat tin boxes. These burn with a fairly even flame and do not greatly decrease in height as they are consumed. The cobalt-chloride paper was cut into appropriate sizes and kept in small and tight tin boxes. In the field the boxes were placed on top of the little stove. The hygrometric papers were in this way properly dried and were kept suitably dry as long as was required. In no case was it possible to dry the papers over the candle flame directly, owing to the almost constant wind, which made it necessary to use a small screen even with the heating apparatus described.

Glass clips with color standards and holding cobalt-chloride paper were placed as controls near the leaves studied. This was found to be advisable, owing to the long reaction-time which many of the leaves were found to have.

In the event that the leaves were too thick to use with the glass clip supplied, a substitute was found by using large metal clips with celluloid in place of the glass.

It was found necessary to add to the glass clip with its rather delicate spring an additional spring clip in order to get firmer attachment to the leaf. This was especially necessary in the case of small leaves. For the purpose a wooden clothes-pin with spring was found to be suitable.

In running a series of tests, several clips were used at one time, and whenever possible also the same leaf and even the same portion of the leaf was studied repeatedly. In this way the course of the transpiring power of the plant could better be determined.

As is essential for the work, the temperature of the air near the leaves being tested was recorded, and such temperatures used in calculating the indices of the transpiring power in the way worked out for the method.¹

But few attempts were made to run the tests during the hours of darkness, in part because it was found to be difficult, if not impossible, even with the aid of a flash-light, to surely distinguish the color reac-

¹ Improvements in the method for determining the transpiring power of plant surfaces by hygrometric paper. B. E. Livingston and Edith B. Shreve. *Plant World*, vol. 19, p. 287, 1918.

tions. Accordingly, the daily course of the observations was from about sunrise to about sunset, when the tests were made at approximately 2-hour intervals.

The transpiration studies were carried out on the following species: At Beaufort West: *Aloe schlechteri*, *Gasteria disticha*, *Grewia cana*, *Gymnosporia buxifolia*, and *Massonia latifolia*. At Matjesfontein: *Aloe striata*, *Cotyledon coruscans*, *C. paniculata*, *Eucalyptus globulus* (?), *Euclea undulata*, *Euryops lateriflorus*, *Protea neriifolia* (Tweedside), *Rhus viminalis*, and *Rhus* sp. (Whitehill). Namib Desert: *Bauhinia marlothii*, *Welwitschia mirabilis*.

BEAUFORT WEST.

ALOE SCHLECHTERI.

At Beaufort West *Aloe schlechteri* (plate 8A) occurs on the north-east upper slopes of a chain of low kopjes which are east and north of that place. Only two groups of a few plants each were seen. Of these, the ones especially studied were growing on a kopje about 2 miles to the north of town. The observations were made on August 15 and 16, at a time when the leaves were turgid and when the species was about to flower.

On August 15 the shade temperature of the air near the *Aloe* selected for study was between 15° C. in early morning and 24° C. about mid-day. The day was fair and dry. There was a strong breeze from the north, which arose about sunrise and continued throughout the day. The cobalt-chloride control did not change in color, and strips of the paper freely exposed to the air changed only to light blue. Three leaves were used. The indices of transpiring power, together with the time of the observations and the reaction-time, are given in table 13, for leaf No. 2, and illustrate those obtained for the two other leaves.

TABLE 13.—*Transpiring power, leaf No. 2, Aloe schlechteri, August 15.*

	Reaction-time, in seconds.	Index of trans- piring power.
7 ^h 37 ^m	300 to 330	0.095
9 7	300 to 420	.065
11 31	510	.030
5 19	840	.019

On the following day the experiments were run during the morning only. The day was fair and a light breeze which lasted all of the forenoon came from southerly points. The humidity of the air was apparently somewhat high, because, upon being exposed to the air, the dark-blue cobalt-chloride papers quickly changed to light blue and to pink. The temperature of the air ranged between 5° and 22° C. Table 14 summarizes the August 16 test on leaf No. 2.

On August 16, three leaves were used, and it was found that, especially in early morning, there was much variation in the readings. On two leaves two clips were read at the same time with widely different results which were not accounted for. But the lowest trans-

TABLE 14.—*Transpiring power, leaf No. 2, Aloe schlechteri, August 16.*

	Reaction-time, in seconds.	Index of trans- piring power.
7 ^h 55 ^m	180 to 330	0.198
9 27	210	.169
9 48	360	.092
11 9	620 to 720	.033

piring power of leaf No. 2 on this day, including the early reading, was very much greater than the highest for the preceding day. The indices at the late morning hours for the two days are, however, about the same. Inasmuch as the humidity was higher on the second day of the observations, and for the entire morning, it was not considered probable that the difference noted was owing to its direct effect on the cobalt-chloride paper by leakage around the clip, for the reason that, as above indicated, the later hours, when the humidity was yet high, the index of transpiring power for the two days was substantially the same. It was consequently concluded that the variation in the index as between the two days was due to actual differences in the transpiring power of the plant. This makes the considerable range of 10 to 1 in the index, which, however, should not be considered the limits of variation, as a lower index would be expected in a more arid season.

GASTERIA DISTICHA.

Gasteria disticha (plate 9) occurs at Beaufort West on the southerly upper slopes of the kopjes near town. Usually it is in association with some large species, as *Lycium* sp., by which it may be “protected” in some fashion. It is a leaf succulent.

TABLE 15.—*Transpiring power of Gasteria disticha.*

	Reaction-time, in seconds.		Index of trans- piring power.	
	Smaller leaf.	Larger. leaf.	Smaller leaf.	Larger leaf.
7 ^h 42 ^m	660	660	0.070	0.070
9 7	660	600	.047	.052
9 28	1,020	900	.030	.034
11 24	1,080	1,040	.022	.023
12 13	1,020	1,040	.019	.013
3 31	1,740	1,980	.010	.009

The transpiration power of *Gasteria* was studied on August 19 and 22. On the first day a reaction-time between 300 seconds in early morning and 3,360 seconds in mid-afternoon was obtained, with an index varying between 0.097 and 0.009. On the following day observations were made on two leaves, a larger and a smaller one, which were assumed to be of unlike age. The smaller leaf was very evidently of the preceding year and the larger one may have been several years old. Table 15 summarizes the leading results of August 22.

It will be seen, therefore, that the transpiring power of the larger (older) leaf and of the smaller (younger) one is about the same. There seems, however, to be a slight difference in that in mid-afternoon the smaller leaf has a relatively small index and at mid-day the opposite is the case. So far as the latter condition is concerned, which is not well indicated by the table, the reaction of the larger leaf at 12^h 13^m was not wholly complete when the reading was made. At 3^h 30^m, however, the paper had changed to pink. In any event, the index of transpiring power of the species was found to be low.

GREWIA CANA.

Grewia cana (plate 7B) is a sclerophyllous shrub with evergreen leaves about 1 by 2 cm. in size, which at Beaufort West occurs sparingly on kopjes, especially on the southern slopes. The leaves are distinctly dorsi-ventral.

The transpiring power of the species was studied August 20, 22, and 23.

On August 20 the test was for the purpose of determining whether the two-leaf surfaces had unlike indices. The results for that day are summarized in table 16, which gives the time of the observations and the indices.

TABLE 16.—*Transpiring power of dorsal and ventral leaf-surfaces of Grewia cana, August 20.*

	Dorsal leaf-surface.	Ventral leaf-surface.
8 ^h 4 ^m	0.020	0.118
9 14	.035	.374
2 50		.234

It, therefore, is clear that the transpiring power of the dorsal surface is low, perhaps indicating cuticular transpiration only, but that of the ventral surface is high. Similar results were obtained on August 22, in which a difference of about 8 to 1 in the index was found between the ventral and the dorsal surfaces of the same leaf.

On August 23 tests were made on the ventral surface only. They were carried out in part on numbered leaves, so that the behavior

of the individual leaf through the day was learned, and this was checked by tests of a number of leaves not used otherwise. Of the numbered leaves, No. 2 was “young” and No. 3 was “old,” at least, the former was smaller than the latter and may have been developed the year the study was carried on. The first tests of the day were made about sunrise and the last were made nearly an hour after the sun had set on the side of the kopje where the plant studied was growing. The day was clear throughout, and the temperature of the air varied from 8° to 23° C. A summary of the results, including the time of observations and the indices of the transpiration power of the ventral surface, is given in table 17.

TABLE 17.—*Transpiring power of Grewia cana, ventral leaf-surface, August 23.*

	Large leaf.	Small leaf.	Leaves all different.		Large leaf.	Small leaf.	Leaves all different.
7 ^h 36 ^m	0.132			4 ^h 50 ^m	0.138	0.092	
9 20		0.201		5 5			0.116
10 12	.160	.152					.116
10 22	.114						.117
11 18	.167	.119					.134
2 25	.237	.207					.145
2 45			0.260	5 47	.090	.111	
			.216	5 55			.141
			.173				.147
			.173				

The first observation, as indicated in the table, was on a large leaf, when an average index of transpiring power of 0.132 was obtained. At the same time another test was run on a large leaf, which was partly protected by a *Gymnosporia* shrub which was close by. This had a reaction time of 480 seconds, the longest of the day, and the index was 0.097.

It was frequently observed that successive tests of the transpiring power of the ventral surface were unlike, although the external conditions were apparently unchanged. Thus at 7^h 36^m the successive reaction-times were 345 and 360 seconds and at 8^h 5^m successive reaction-times of 240 and 270 seconds were obtained on the same leaf. At 9^h 40^m two tests were made 4 minutes apart on the same leaves and on the *same leaf area*. In the case of a smaller leaf the reaction-times were 90 and 150 seconds, and in a larger leaf they were 100 and 180 seconds. The differences in the reaction-time are consequently in the direction above noted. Such results indicate that in some way the presence of the glass clips disturbs the series of events which accompany water movements within the plant and through which the moisture is brought into contract with the surrounding air. What these may be was not studied. But it is clear that the clips cut out temporarily the saturation deficit of the atmospheric air as an imme-

diate factor influencing water movement within the plant, as well as to greatly change the character of the light falling on the leaf-surface.

GYMNOSPORIA BUXIFOLIA?

Gymnosporia buxifolia (plate 7A, 7C)¹ is an evergreen shrub which occurs at Beaufort West, on the southern slope of kopjes near town. The leaves are 3 or 4 cm. long and about 1 cm. in width, and the two leaf-surfaces are unlike in appearance. The specimens studied were growing in association with *Grewia cana*, of which the transpiration power was treated in the preceding section, and to which it bears resemblance in its general habit of growth.

The transpiring power of *Gymnosporia* was studied on August 5, 6, 12, 13, and 17; 89 observations were made, special attention being paid to possible differences in the reaction of the two leaf-surfaces. All of the tests were made during the hours of sunlight, although those on August 13 were begun at about sunrise. The days were without cloud. On the 17th there was a strong breeze and the air was relatively very dry. It requires 480 seconds for the dry and dark-blue cobalt-chloride paper to fade to light blue when freely exposed to the air.

Preliminary tests did not show consistent differences in the transpiring power of the leaf-surfaces, although the dorsal appeared to have the larger index. Table 18, in which the time of observation and the indices of transpiring power are given, summarizes the results of August 13.

TABLE 18.—*Transpiring power of dorsal and ventral leaf-surfaces, Gymnosporia buxifolia, August 13.*

	Dorsal leaf-surface.		Ventral leaf-surface.	
	Leaf No. 1.	Leaf No. 2.	Leaf No. 3.	Leaf No. 4.
7 to 8 hours...	0.142	0.137	0.117	0.095
9 to 10 hours...	.133	.146	.128	.078
11 to 12 hours...	.240	.240	.202	.061
12 to 1 hours...	.100	.100	.151	.098
2 to 3 hours...	.072	.108	.103	.056

On August 17 lower values were obtained. The reaction-time varied from 210 mid-forenoon to 3,360 seconds in mid-afternoon, and the index of transpiring power ran from 0.023 to 0.065. These do not represent possible extremes of the day, because readings were not made in early morning, when a high index might be expected. At 10^h 25^m the dorsal surface of leaf No. 3 had an index of 0.065, and the ventral surface of No. 4, a similar leaf, had an index of 0.030 and 0.052.

¹ Dr. Marloth informs me that this may be *G. integrifolia* (L. F.) Szysz.

At 11^h 55^m the index of the dorsal surface of leaf No. 2 was 0.023, and at 12^h 7^m that of the ventral surface of the same leaf was 0.041. These differences in the size of the index of transpiring power as between the dorsal and the ventral surfaces are not sufficiently large or consistent to make it appear likely that the leaves are physiologically dorsiventral, although they have this appearance. The structure will be commented on in another place.

MASSONIA LATIFOLIA.

At Beaufort West the acaulescent *Massonia latifolia* (plate 9) with water storage in the subterranean organs occurs on the southern slopes of a kopje about 2 miles north of town. The opposite leaves lie freely on the surface of the ground and are about 10 by 20 cm. in size and possibly 4 mm. in thickness.

The transpiration power of the plant was observed on August 19 and 22, when numerous tests were made. On the first day attention was given to determination of possible differences in the two surfaces in transpiration power. On the second day only the upper leaf-surface was used. The time of observation on August 19 and the calculated indices are summarized in table 19.

TABLE 19.—*Transpiring power of Massonia latifolia, August 19.*

	Index of upper leaf-surface.	Index of lower leaf-surface.		Index of upper leaf-surface.	Index of lower leaf-surface.
9 ^h 57 ^m	0.171		3 ^h 58 ^m	0.088	
10 20		0.125		.097	
		.154	4 10		0.088
		.257			.081
10 42	.052		4 22		.065
11 8		.033	4 34	.052	

On August 22 the upper surface of 4 leaves was used. The first observations were made about 35 minutes before the sun rose on the south side of the kopje and were continued until between 12 and 1 o'clock. The day was clear and the temperature of the air varied from 7° in early morning to 20° C. at midday. Reaction-times between 150 and 2,500 seconds were obtained, with corresponding differences in the index of transpiring power. Table 20, giving the time of observations and the indices, summarizes the results.

TABLE 20.—*Transpiring power, dorsal leaf-surface, of Massonia latifolia, August 22.*

	Leaf No. 1.	Leaf No. 2.	Leaf No. 3.	Leaf No. 4.
7 ^h 26 ^m	0.0206			0.018
9 ^h to 10 ^h		0.048	0.046	.047
11 ^h to 11 ^h 37 ^m ...	.161	.114	.100	.0503
	.050	.047		
12 ^h 15 ^m		.066	.066	.083

It appears, therefore, that the index of transpiring power is less in early morning than in late forenoon, and that during so short time its variation may be considerable.

There was no apparent difference in transpiring power between the lower and protected surface and the upper exposed surface.

MATJESFONTEIN.

The species used at Matjesfontein as a center were situated in part on veld and in part in an abandoned park in town. In the latter, water from the rains only was received. *Aloe striata*, *Cotyledon coruscans*, *C. paniculata*, *Eucalyptus globulus?*, and an undetermined weed belonging to the Chenepodiaceæ were studied in the location last named. *Cotyledon paniculata* was also studied on the veld, as were *Euclea undulata*, *Euyrops lateriflorus*, and *Rhus viminalis*. A species of *Rhus* was also studied at Whitehill, and *Proteaneriifolia* at Tweedside.

ALOE STRIATA.

The leaf succulent *Aloe striata* is a large-leaved species occurring further east in the Great Karroo, which has been introduced, together

TABLE 21.—*Transpiring power of Aloe striata, August 24.*

	Younger leaf.	Older leaf.
6 ^h 6 ^m to 18 ^m	0.051	0.060
8 ^h 16 ^m to 20 ^m	.051	.040
10 ^h 16 ^m to 20 ^m	.016	.028
	^a .019	
	^a .018	
10 ^h 2 ^m to 32 ^m	.011	.010
	.012	
12 ^h to 12 ^h 15 ^m	.012	.012
1 ^h 50 ^m	^b .025	^b .008
4 ^h 2 ^m to 15 ^m	.013	.010

^a Two leaves not used at any other time.

^b The index for the younger leaf is somewhat too high, and that of the older leaf somewhat too low.

with numerous other Karroo species, in the park at Matjesfontein. Here it grows well, although the rainfall is less than in the Gough,¹ and, moreover, occurs mainly at another season.

Several tests were made on *Aloe striata*, but only those of October 24 will be described. Sunrise occurred on that day about the time of the first observations. The morning was clear, but about noon light clouds appeared and the sky became hazy. The temperature of the air varied between 8° C. in early morning and 34° C. in mid-afternoon. Two leaves were mainly used. Of these, one was smaller and probably younger than the other. The time of the observations and the index of the transpiring power are given in summarized form in table 21.

¹ The central portion of the Great Karroo. A Hottentot word said to signify "empty, bald, naked, or nothing," according to Bews.

COTYLEDON CORUSCANS.

Cotyledon coruscans (plate 24c) is a leaf succulent of rather wide distribution in the Karroo. The evergreen leaves are fairly thick and about 7 by 14 cm. in size. The species is native at Matjesfontein, where it occurs in stony places, on kopjes, etc.

FIG. 11.—Average indices of foliar transpiring power at 2-hour intervals, 8^h a. m. to 10^h p. m. A, *Aloe schlechteri*; B, *Gasteria disticha*; C, *Aloe striata*; D, *Cotyledon canescens*.

The transpiration power of the species was studied October 5, 6, and 13. Tests were made on specimens growing on the edge of the town. Controls were used. On October 5 and 6 the weather was fair and the air was dry, so that the control slips changed little or not at all. On October 13, however, there were some clouds and the controls underwent reaction to light blue and to pink within 30 minutes. Table 22, in which the observation time and the index of transpiration power are given, summarizes the leading results.

It will be noticed that there was a certain degree of agreement in the hourly course of the index of transpiring power, during the hours of

TABLE 22.—*Transpiring power of Cotyledon coruscans.*

	Oct. 5.	Oct. 6.	Oct. 23.
7 to 8 hours....	0.0140	0.0120	
8 to 9 hours....			0.0099
9 to 10 hours...	.0100	.0100	.0070
10 to 11 hours...	.0073	.0096	
11 to 12 hours...			.0097
12 to 1 hours....		.0110	
2 to 3 hours....	.0033	.0053	
		.0062	
4 to 5 hours....		.0110	.0080
5 to 6 hours....		.0090	
		.016	
6 to 7 hours....	.0160		
7 to 8 hours....		.016	
9 to 10 hours...	.0160		

daylight at least, in the three days. At or before sunrise, and about or after sunset, the index is relatively high, but it falls during the early portion of the afternoon.

There is also a striking correspondence, but not exact agreement, between the reaction of the control and that of the test clips. When the indices were low the reaction-time of the control was long. But in certain tests, as at 9^h 50^m on October 13, the reaction-time of the test clip, from dark to light blue, was 2,820 seconds, while the reaction time of the control, dark blue to pink, was 6,000 seconds. The control was exposed to the wind, but the plant was sheltered. It is evident, therefore, that while the transpiring power of the plant was not large, some transpiration in fact did occur.

COTYLEDON PANICULATA.

Cotyledon paniculata (plate 18) occurs sparingly on kopjes in the vicinity of Matjesfontein. This species has features of much interest. As is shown elsewhere in this study, it is a stem succulent

FIG. 12.—Average indices of foliar transpiring power at 2-hour intervals, 8^h a. m. to 10^h p. m. A, *Cotyledon paniculata*; B, *Massonia latifolia*.

having fleshy stem and branches, and fairly fleshy leaves which are deciduous. Leaves are present in winter and early spring, but they fall with the approach of the warm season and the species passes the summer in a leafless condition. In September, when studies were begun on the species, the leaves appeared to be turgid and photosynthetically active, but in middle of October, and especially later in the month, those on some specimens were beginning to give evidence of preparation for early falling.

The specimens used in the studies were mainly in the abandoned park in town, but some observations were also carried out, in October only, on plants growing on a kopje about 2 miles distant. Studies on the transpiration of *C. paniculata* were made on September 21, 26, and 27, and October 4, 13, and 19. A running account will be given of those which are considered most important, a résumé of the balance, and a summary of all.

The plant used September 21 was growing on a small pile of rather small rocks, where it had been brought from a nearby kopje. The main stem was about 8 cm. in diameter and bore fleshy branches. The leaves studied were either about 8 by 5 cm. or about 4.5 by 2.2 cm. in size, the smaller being in general nearer the top of the plant. The large leaves were about 5 mm. in thickness and were not very turgid; at least they were not easily broken when bent. Young shoots bearing

spatulate and small leaves were appearing. Only the leaves of the preceding season, however, were used in the studies.

On September 21 tests were made between 6^h 35^m in the morning and 4^h in the afternoon. Sunrise occurred at about 6^h 45^m. There was sunshine until noon, when light clouds appeared, and much of the afternoon was somewhat overcast.

The transpiration power of the dorsal surface only of the leaves was studied.

Four tests were made about sunrise, with reaction-time of 540, 700, 720, and 720 seconds. The average index of transpiring power was 0.0648. At 7^h 44^m and 8^h 2^m the reaction-time was found to vary from 720 to 1,020 seconds, and the average index was 0.033.

From 9^h 29^m three tests were made, giving reaction-time of 660, 1,020, and 1,140 seconds. The average reaction-time of the last two is 0.0163, that of the first is 0.023. Of the three observations, the longest is noted as being "good," the intermediate one as possibly having been continued overlong, but the first was "satisfactory."

At 10^h 18^m to 10^h 24^m the reaction-time for three tests was from 780 to 1,260 seconds and the average index was 0.0149. At 10^h 24^m a single test (probably of an old leaf) had a reaction-time of 2,160 seconds, at a temperature of 24° C. The index of the transpiring power for this test was, therefore, 0.0072.

Between 11^h 44^m and 12^h 7^m three tests gave reaction-time of 600, 600, and, on an old leaf, 1,280 seconds. The index of the former is 0.028 and of the latter 0.0098.

Three tests, beginning with 2^h 14^m, gave reaction-time of 1,800 to 2,100 and an average index of 0.0063.

And, finally, three observations beginning at 4^h, when there were clouds, gave reaction-time between 1,320 and 1,740 seconds and an average index of the transpiring power of 0.0147.

During the day observations were also made on the transpiring power of a species of chenopod which was growing within 1 meter of the species of *Cotyledon* studied. An index between 0.075 and 0.19 was obtained for this plant.

On September 26 observations were made from 6^h 45^m in the morning, that is, from about sunrise, until 5^h 3^m in the evening. The day was with sunshine throughout and very dry. Control slips were used paralleling each test period. They did not change in shade of color at any time during the day, except only that at about midday they appeared to get somewhat lighter than when they were put out.

At 6^h 45^m five tests were made. The same plants were used as on the preceding day. After 60 minutes there was no color change. At 9^h 5^m tests were again made. The cobalt-chloride papers at the end of 50 minutes were pink on the edges, but light-blue on the inside. The control was unchanged.

Five tests were again made at 11^h 5^m, when a reaction-time of 1,800 and 2,400 seconds was noted, and at 11^h 16^m a third test gave a reaction-time of 2,880 seconds. In the first instance the index was 0.0011, and in the last test it was 0.0086.

At 2^h 15^m a reaction-time, the average of five tests, of 2,280 seconds was obtained, giving 0.0077 as the index of transpiring power.

Two observations, of two tests each, were made at 4^h 13^m, when the average-reaction time was 1,620 seconds, and the index was 0.0109. This was on a relatively young leaf. At the same time a series was run on an older leaf, in which the reaction-time was 2,940 seconds, giving the index as 0.0059.

At 5^h 3^m the index was determined to be 0.006.

Observation about 5 o'clock on the transpiration of a chenopod growing near showed reactions between 180 and 420 seconds, with indices between 0.11 and 0.041.

The tests made on September 27, which was also a clear, dry day, gave essentially the same results as on the preceding days, although the first observation was not made until 8^h 25^m.

The index of the transpiring power for the earlier tests was 0.011, which was the average of five observations. At about 10 o'clock the index had fallen to 0.0055, but this is probably too low, as the reaction was somewhat beyond the end customarily used. At about noon the average index of five tests was 0.01. At 2^h 9^m the average of five tests gave an index of 0.009. At 4^h 7^m five tests were run, of which two gave an index of 0.0048 and one 0.0087. At 6^h 7^m the final observations were made, at which time the average index for five observations was 0.012.

At the time the observations were being made on the cotyledon, tests were run on leaves of *Eucalyptus globulus* ? and on a species of *Chenopodium*, both of which were within about 150 cm. of the cotyledon. The index of transpiring power of the chenopod at 10 o'clock was 0.265, and that of an old and round leaf of the *Eucalyptus* was 0.168, while that of another *Eucalyptus* leaf, which was younger, was 0.0808. At about 4 o'clock a round and old leaf of *Eucalyptus*, the same as above used, gave an index of 0.082, and the younger round leaf an index of 0.061. The older leaf, at 6^h 12^m had an index of 0.0248.

On October 3 observations were begun at 6^h 45^m, but a heavy wind sprang up with the rising of the sun and the humidity of the air rapidly increased, so that the control slips changed in color fairly quickly, as did also those on the plants studied. The tests were, therefore, abandoned for the time.

The index of the transpiring power of the *Cotyledon*, as determined on October 4, was for each period given as follows: 7^h 50^m, 0.013; 9^h 44^m, 0.019; 10^h 34^m, 0.011; 12^h 15^m, 0.011; 2^h 8^m, 0.0089; 4^h 17^m, 0.01; and 5^h 43^m, 0.02. Control clips were used during the day and they showed no or slight change in color.

On October 13 the weather conditions were somewhat variable. The morning was clear, but toward mid-day light clouds appeared and the air was as usual dry, although there was some lack of uniformity in this regard. For example, in early morning the controls changed in color little, if any, but at 11^h 25^m a control paper underwent complete reaction, that is, to pink, within a few minutes. In the afternoon, however, the controls changed only slightly.

Leaves Nos. 1, 2, 6, 8, and 9 were studied. Before and about sunrise five tests were made of which the earliest, 6^h 5^m gave the highest index, namely, 0.05, which was of Nos. 6 and 8. A half hour later No. 2 had an index of 0.045. But the balance had indices between 0.023 and 0.029.

At 8^h 8^m the index of Nos. 1 and 2 was 0.023, and of Nos. 6 and 8 was 0.0152. The control which was running parallel to these tests did not show any change in color.

The average index for three tests made at 9^h 35^m was 0.017. At this time the control had changed but slightly.

At 11^h 20^m three observations were made. Of these No. 9 had an index of 0.0091, and Nos. 2 and 6, 0.0073. The control during this period was completely changed in color, that is, to pink.

At 2^h 12^m the average index of Nos. 1, 2, and 6 was 0.014. The control had changed slightly in color.

The final test was made at 4^h 8^m with Nos. 2, 6, and 9, when the average index was found to be 0.014. The control had partly changed during the period.

On October 19 a few tests were run on two plants of *Cotyledon paniculata* growing on a kopje about 2 miles northeast of Matjesfontein. They were about 1 meter high. The diameter of the stem of one was about 16 cm. and that of the other about 39 cm. The leaves of the tips of some of the branches were somewhat yellow, but those used were green and apparently quite vigorous.

Observations were made 2^h 35^m, 3^h 5^m, and 4^h 35^m. The controls did not change in color during the tests.

At 2^h 35^m six leaves were used. They had an average reaction-time of 1,500 seconds and an average index of transpiring power of 0.0093. The average reaction-time of the next following observation was 2,280 seconds and the index was 0.0072. At 4^h 35^m the average reaction-time of three leaves was 0.011. The reaction had been carried somewhat past the light-blue color of two other leaves. It is evident that the index of transpiring power of the species growing on the kopje was not far from that of the species in the neglected park at Matjesfontein, so that the results with the latter plants can be interpreted as also applying to species in the veld.

It will be seen from the summary of the indices of transpiring power given in table 23 that the average index for *Cotyledon paniculata*

decreases from early morning, and fairly quickly so, so that by mid-forenoon it may be at the lowest for the day. It increases again toward evening.

As in certain other species, particularly with *C. coruscans*, there was sometimes noted a parallel in behavior as between the control and the hygroscopic paper used in the tests. For example, in early morning on September 26 the reaction-time was more than 3,600 seconds, and there was no color change in the control. But, on the other hand, on the following day, at 11^h 55^m, the reaction-time was 1,550 seconds, and only slight change was seen to have taken place in the control.

Tests of the transpiring power of *Cotyledon paniculata*, *Eucalyptus globulus*?, and of a species of chenopod, which were run synchronously on September 27, gave interesting comparative results. Thus the reaction-time of *Cotyledon* was 3,600 seconds, that of the chenopod was 180 seconds, and that of old and round leaves of the *Eucalyptus* was 120 and of younger round leaves 240 seconds. The indices of the transpiring power of these tests were 0.0055, 0.117, 0.176, and 0.088, respectively. This series suggests, which is further strengthened by the table of indices and that given in connection with the

TABLE 23.—*Transpiring power of (indices) Cotyledon paniculata.*

	Sept. 21.	Sept. 26.	Sept. 27.	Oct. 4.	Oct. 13.	Oct. 19.
6 to 7 hours.....	0.064	0.0006			0.011	
7 to 8 hours.....	.035			0.019		
8 to 9 hours.....			0.011		.019	
9 to 10 hours.....	.017	.009	.005	.021	.008	
10 to 11 hours.....	.011			.008		
11 to 12 hours.....	.017	.008	.009		.008	
12 to 1 hours.....				.010		
2 to 3 hours.....	.005	.007	.009	.008	.015	0.009
3 to 4 hours.....						.007
4 to 5 hours.....	.014	.005	.006	.009	.014	.011
5 to 6 hours.....				.016		
6 to 7 hours.....			.012			

paragraphs on *Eucalyptus*, that the highest index of transpiring power of the *Cotyledon* is usually lower than the lowest of the *Eucalyptus*, and that the difference at the same time may in fact be very considerable indeed.

EUCALYPTUS GLOBULUS?

As has already been mentioned, *Eucalyptus globulus*? occurs in an abandoned park at Matjesfontein. It was not irrigated and apparently had not been irrigated for several years previous to my visit. The trees are 15 meters, more or less, in height and at the base are young shoots bearing the juvenile type of leaves. Both the narrow and

the round forms of leaves were studied as an aside while the transpiring power of *Cotyledon coruscans* and *C. paniculata* was being investigated.

Observations on the transpiring power of *Eucalyptus* were made on September 27 and October 4 and 13. The results of the tests of September 27 have already been referred to. It was stated, in brief, that the index of the transpiring power of round and old leaves at about 10 o'clock in the morning was 0.168, and that of a younger leaf was at the same time 0.080. In the afternoon at about 4 o'clock the index of the old leaf was 0.082 and of the younger leaf was 0.061. At about 6 o'clock the index of the older leaf was 0.0248.

On October 4 the observations on *Eucalyptus* were made between about noon and before 6 o'clock in late afternoon. Four leaves were used. Of these Nos. 1 and 2 were round but mature leaves growing on a young shoot. They were about 3.5 by 4.5 cm. in size. Leaves 3 and 4 were of narrow type and were on an old branch. No. 3 measured 4.4 by 8.5 cm. and No. 4 was 9 by 4.2 cm.

At 11^h 50^m the average reaction-time of several readings of leaves 1 and 2 was 60 seconds, while that of No. 3 was 185 seconds, giving the index of transpiring power of 0.32 in the former instance and of 0.098 in the latter.

TABLE 24.—*Transpiring power of Eucalyptus globulus?*, October 13.

	Leaf No. 1.	Leaf No. 2.
6 ^h 37 ^m	0.082	0.082
8 15	.085	.050
9 40	.072	.050
11 27	.097	.075
2 18	.184	.070
4 12	.095	.025

Leaves Nos. 1 and 2 at 2^h 10^m had a reaction-time of from 80 to 90 seconds. The index of transpiring power was 0.19. At 2^h 25^m leaves Nos. 3 and 4 had a reaction-time of 150 seconds and an index of 0.104. At 4^h 20^m the index of reaction-time of Nos. 1 and 2 was 0.0193. At this time the reaction-time of leaf No. 4 was 100 and of No. 3 was 300 seconds, giving the indices of 0.16 and 0.054. The final reading was at 5^h 45^m, at which time leaves Nos. 1 and 2 had a reaction-time of 59 and 49 seconds and an average index of 0.36. The reaction-time of leaf No. 4 at this time was 120 seconds and the index was 0.13.

On October 13 leaves Nos. 1 and 3 were used. Observations were made between 6^h 37^m in the morning and 4^h 12^m in the afternoon. The character of the day has been characterized in connection with an account of the transpiring power of *Cotyledon paniculata*. Table 24 gives the indices with the hour of each observation.

It will be seen, therefore, that except for the early morning reading, the index of transpiring power of the mature (elongated) form of leaf is the smaller at each observation. Comparing the indices of *Eucalyptus* with those for *Cotyledon paniculata*, which were for the same day, it will be found that those of the latter are consistently below the indices of the mature form of *Eucalyptus* leaf.

EURYOPS LATERIFLORUS.

The shrub *Euryops lateriflorus* (plate 15) occurs sparingly on a rocky outcrop on the outskirts of Matjesfontein. The leaves are coriaceous, about 6 by 15 mm. in size, and are closely appressed to the branches. They are abundant. The transpiring power was studied on several days, but the results of observations made on October 14 and 15 need only be given.

The placing of the leaves by which the dorsal surface is pressed closely against the upright branches, with the effect that the ventral surface only is fully exposed to the sunlight and the air-currents led to the supposition that the two leaf-surfaces might have unlike transpiring power. Accordingly observations were made on both surfaces.

On October 14 the day was fair and the controls showed that the air was fairly dry. Wind came from the westerly direction. Sunrise was about 6^h 10^m, about an hour after which the observations were begun. They were continued until 6 o'clock in the evening. The leading results are given in table 25.

TABLE 25.—*Transpiring power of Euryops lateriflorus, October 14.*

	Dorsal leaf-surface.	Ventral leaf-surface.
7 ^h 34 ^m	0.028	0.057
9 23	.029	.032
9 47	.033	.028
11 34	.045	.030
1 53	.030	.030
2 22	.023	.023
4 31	.032	.029
6	.018	.015

On the following day, in order to further test the transpiring power of the two leaf-surfaces, observations were conducted on both surfaces of different leaves and of the same leaf. Tests also were made of leaves which had been in the direct sunlight for a few minutes as opposed to such as had not as yet been in the direct sunlight. The day was about as the preceding one in that the sun was not obscured by clouds and it was fairly dry. The shrub was in full sunshine at 6^h 22^m.

At 5^h 57^m the clips were placed on the dorsal and on the ventral sides of two separate leaves which were on the side of the shrub away

from the light. The index of the dorsal surface was determined to be 0.032 and of the ventral surface 0.025.

At 6^h 30^m the clips were placed on the two surfaces of different terminal leaves, which had been about 20 minutes in direct sunshine. The dorsal surface side gave an index of 0.192 and the ventral surface an index of 0.129.

At 6^h 42^m a long strip of the hygrometric paper was bent and attached to the leaf, so that one portion was on the dorsal surface and the other portion was on the ventral surface. This was held in position by a glass clip with color standard as in the usual way. At the expiration of 300 seconds the reaction of the portion on the dorsal side was complete light blue, while the reaction of the portion of the paper on the ventral side was not wholly carried through. The experiment was repeated at 8^h 8^m and later with similar results.

At 7^h 55^m separate leaves on the shaded side of the shrub were tested, with the following results: The index of transpiring power of the dorsal surface was 0.167. At 8^h 56^m the index of the ventral surface was 0.100.

At 9^h 15^m three tests were made, of which two were on separate leaves in the shade and one was of a terminal leaf that had been in the sun. In the latter instance one strip of paper was bent and clamped on both sides of the leaf, as earlier in the morning. Of the leaves in the shade, the dorsal surface had an index of 0.052 and that of the ventral surface was somewhat less. But of the single terminal leaf, which had been in the direct sunlight, the index of the two surfaces was the same, that is, 0.091.

The ventral leaf-surface of *Euryops lateriflorus*, therefore, has an index of transpiring power which may or may not be lower than that of the dorsal surface. There appears to be some sort of regulatory control of the transpiring power of the lower surface which is absent or not so pronounced on the dorsal surface. In any event the differences in transpiring power between the two leaf-surfaces is not so striking as in certain other species, as, for example, *Grewia cana*, *Rhus viminalis*, or *Protea neriifolia*.

EUCLEA UNDULATA.

Euclea undulata is a shrub with small coriaceous leaves. At Matjesfontein it occurs on kopjes. Only one series of observation were carried out on *Euclea*, but they gave certain results of interest and will be mentioned.

The specimen observed was growing on the summit of a kopje about 2 miles from town and not far from the *Cotyledon paniculata* which was studied the same afternoon, i. e., October 19. The day was warm, 25° C. shade temperature, and dry. The control slips did not undergo color change during the tests.

At 4^h 8^m slips were attached to the dorsal and ventral surface of 5 leaves. The cobalt-chloride paper on the ventral surface changed color in 5 minutes, but that on the dorsal surface had changed slightly, if at all, at the end of 24 minutes. The index of transpiring power of the ventral surface was 0.046 and that of the dorsal surface less than 0.0097. It is evident, therefore, that the specimen studied had a relatively high rate of transpiring power, but that there was practically no loss of moisture from the dorsal surface of the leaves.

RHUS SP. AND R. VIMINALIS.

Two species of *Rhus* were studied. Of these one is a tree, *Rhus viminalis*, which grows along the streamway at Matjesfontein, and the other is a shrub which is apparently confined to kopjes. This last was observed at the Karroo Botanical Gardens, Whitehill, where it is undisturbed and under quite natural conditions.

TABLE 26.—*Transpiring power of Rhus viminalis, October 20.*

	Dorsal surface of leaf.	Ventral surface of leaf.
6 ^h 16 ^m	0.0452	0.1590
11 ^h	.0337	.2885
2 ^h	.0220	.1137
4 ^h 32 ^m	.0096	.1020

Although the tests on *R. viminalis* were carried out on several days, those of October 20 only will be given. The pendent leaves of the species are long and narrow, about 10 cm by 7 mm. They are evidently physiologically dorsi-ventral, even if the two leaf-surfaces are not in appearance strikingly unlike.

On October 20 the air was somewhat humid in the morning, as was indicated by the reaction of the control papers within a period of 900 seconds, but in the afternoon the air was dry. The tests were begun at 6^h 16^m and were continued until 4^h 33^m. Both leaf-surfaces were studied. The leading results are summarized in table 26, in which the indices and the time of the observations are given.

TABLE 27.—*Transpiring power of Rhus sp., October 21.*

	Dorsal surface of leaf.	Ventral surface of leaf.
6 ^h 40 ^m	0.113	0.378
7 8	.031	.204
7 32	.100	.134
8 42	.078	.235
9 6	.055	.160

The observations on the transpiring power of *Rhus* sp. at Whitehill were made on October 21. The control slips did not undergo color change during the hours of the tests. The leaves of this species are approximately 10 by 25 mm. in size, with unlike dorsal and ventral surfaces, although in appearance this is not especially well marked. The observations were made between 6^h 40^m and 9^h 6^m. For the first two periods old leaves were used; in the following the leaves were young. The final tests, at 9^h 6^m, were made on large shade leaves, with results as given in table 27.

It is evident that in both species the transpiring power of the two surfaces of the leaves is strikingly unlike and that transpiration is carried on largely on the ventral surface. The difference is especially marked in old leaves. The ratio in transpiring power between the ventral and dorsal surface is 1 to 3, or even greater in *Rhus viminalis*.

PROTEA NERIIFOLIA.

Protea neriifolia (plate 19A) occurs at Tweedside, altitude 3,291 feet above sea-level, and about 13 miles west of Matjesfontein.

The shrub has upright branches on which the old leaves take an upright position, with the upper or dorsal surface facing the branch and the ventral surface without especial protection. The young leaves stand out somewhat from the branches that bear them. The old leaves are glabrous, but the young leaves are tomentose. The mature leaves are about 2.8 by 8.3 cm. in size and the two leaf-surfaces are not greatly unlike in appearance.

FIG. 13.—Average indices of foliar transpiring power at 2-hour intervals, 8^h a. m. to 10^h p. m. A, *Protea neriifolia*; B, *Rhus viminalis*; C, *Euryops lateriflorus*; D, *Grewia cana*; E, *Gymnosporia buxifolia*.

Observations on the transpiring power of *Protea* were made October 23 between 11^h 20^m and 3^h 20^m. The day was clear and the air was dry. There was no wind. Three leaves were mainly used. Of these No. 1 was 20 by 63 mm. and was situated immediately below the tip of the branch. Leaf No. 2 measured 18 by 67 mm. and was 10 cm. from the branch-tip. And leaf No. 3 was 3 by 19 cm. in size and had about the same relative position as No. 2. In addition to these an old leaf, which was 50 cm. from the tip and which measured 26 by 83 mm., was used and also a young leaf which was 14 by 42 mm. in size. Table 28 is a summary of the leading results of the observations.

TABLE 28.—*Transpiring power of Protea neriifolia.*

	Dorsal leaf- surface.	Ventral leaf- surface.	
12 ^h	0.473	0.107	Leaf No. 2.
12 ^h 25 ^m		.302	Leaf No. 1.
Do.....		.268	Do.
2 ^h 45 ^m	.376		Leaf No. 1, near base.
Do.....	.187		Leaf No. 1, near tip.
Do.....		.125	Leaf No. 1, near base.
Do.....		.094	Leaf No. 1, middle of leaf.
3 ^h 15 ^m	.347	.205	Old leaf.
3 20	.251	.161	Young leaf, 42 mm.

It appears from the few tests made that in old leaves with the upright growth habit the index of the transpiring power of the ventral and outer surface is less than that of the dorsal and protected surface. This was also the case with the young leaf. The young leaf which was studied at the same time the old leaf was used, 3^h 15^m to 3^h 20^m, had a heavy tomentum, while the old leaf was glabrous. The smaller index of the former is striking and suggests the possible importance of the tomentum as a protective covering to the leaf. On the dorsal surface, at least, the index for an area near the base is greater than for an area near the tip of the leaf. Finally, the high index of transpiring power of *Protea neriifolia* is directly related to the occurrence of the species in relatively moist habitats.

NAMIB.

WELWITSCHIA MIRABILIS.

A single series of tests on the transpiring power of *Welwitschia* was carried out on June 28, at which time also the transpiring power of a broad-leaved legume, *Bauhinia*, which was growing not far distant, was observed. Although thus limited in number, the tests should be of a certain value because of the interesting species, especially of *Welwitschia*, and of the intensely arid nature of the habitat.

The habitat of *Welwitschia* is about 50 km. east from Swakopmund and about 8 km. south of the Swakop River. It appears to be a wide

wash which inclines gently toward the north. Here and there in the slope are inconspicuous channels which would escape attention but for the fact they carry narrow lines of low shrubs, which are not numerous. For the most part the surface of the ground is quite devoid of vegetation. Among the plants to be found in these channels are species of *Arthræua*, *Asclepias*, *Bauhinia*, and *Zygophyllum*. *Welwitschia*, of which 5 scattering representatives were seen, occurs on the plain and without reference to the drainage-channels; of these, 3 were possibly 2 mm. from tip to tip, 2 were smaller, and none of them projected above the surface of the ground to a height exceeding about 15 cm.

The specimen studied was one that bore cones (plate 2). The leaves were about 1 meter in length. The leaf-tips were bleached to a gray color and had been whipped into strands by the wind, but the central and basal portion was whole and of a bright grass green. There appeared to be no pubescence on the leaves, which, however, are provided with a double epidermis and with deeply sunken stomata. The tests of the transpiration power of *Welwitschia* were carried out about 9 o'clock in the morning. The day was clear and there was no unusual wind. The temperature of the air was 23° C. The upper leaf-surface, near the base, was used. The average reaction-time of several tests was 120 seconds, giving an index of 0.1383.

BAUHINIA MARLOTHII.

Among the shrubs growing near *Welwitschia*, as above remarked, was *Bauhinia marlothii*, which was conspicuous from the fairly relatively large size of the leaflets, which measured 2 by 3 cm., more or less. Tests carried out on *Bauhinia* showed the same reaction-time as *Welwitschia*, that is, 120 seconds, giving the index also as 0.1383.

SUMMARY.

Although the studies on the transpiring power of the species used are at best fragmentary, in part from the small number and in part from the fact that the work was confined to the winter and early spring, nevertheless they offer suggestions of some interest and indicate that further investigations along the same lines should bring fruitful results.

It was early observed that under certain conditions of the relative humidity of the air, as when it was fairly high, or, on the other hand, fairly low, there was often a disturbing parallel in the reaction-time between the hygroscopic papers attached to the plant and similar papers not so attached. This led to the use of control slips, by which it was possible to detect the direct influence of the humidity of the air, if any, to the end that questionable results might be discarded.

To a certain and possibly limited extent, and possibly limited to certain types of perennials, there may be a real parallel between the

relative humidity of the air and the transpiring power of plants. Bakke, for example, has stated that "a rise in evaporation will give an increase in the transpiring power,"¹ that is, in the species used by him. Such was thought to be probably true in some of the Karroo plants examined, particularly in *Grewia cana*, *Gymnosporia buxifolia*, and *Rhus viminalis*; but whether the principle applies to Karroo species with smaller transpiring power remains to be determined.

In general the older leaves appear to have a higher index of transpiring power than young leaves. In *Protea neriifolia*, where such was observed to be the case, the young leaves are heavily tomentose. In an introduced *Eucalyptus* there was found to be a difference in the index of mature leaves, which depended on the leaf-type. Elongated leaves, on old wood, have a lower index than mature round leaves on young wood.

In *Grewia*, *Euclea*, and *Rhus* the two leaf-surfaces have unlike transpiring power. The index is always larger for the ventral surface. Moreover, the course of transpiring power of the dorsal surface appears to fairly parallel the variation in the humidity of the air, which, indeed, may be the case, for the reason that stomata are absent in these species from the dorsal leaf-surface.

In *Protea* the leaves assume an upright position, with the ventral surface facing outward. In this position the dorsal surface is relatively well protected, while the ventral surface is quite exposed. A somewhat similar leaf position is to be found in *Euryops lateriflorus*, although in this case it is not so well marked. In *Rhus viminalis* the leaves do not appear to have a fixed position. Horizontality of the leaves of *Grewia cana* is the rule. With the apparent exception of *Rhus*, therefore, there is a striking relation between leaf orientation as regards light and other external features, and the surface with the higher transpiring power.

In studying the transpiring power of relatively large leaves, such especially as those of *Protea neriifolia*, it was found that to a certain extent the index varied with the position of the clip on its surface. Further, in other species, especially in *Grewia cana*, successive readings made a few minutes apart gave unlike results, but, however, results which were in a certain way consistent. Thus, in one instance, two successive readings gave reaction-times of 100 and 180 seconds, another set of two readings gave 240 and 270 seconds, and a third set, in which the same leaf area was carefully used, gave 90 as the first, and 4 seconds later 150 seconds as the reaction-time. Such results indicate that in some manner the presence of the closely applied glass clips disturb the series of events which accompany or cause water movements within the leaf and its final release to the surrounding atmospheric air. Whatever may be the direct effect on these physiological features, it is clear

¹ Determination of wilting. A. L. Bakke. Bot. Gaz., vol. 66, p. 105, 1918.

that in the first place the glass immediately operates to modify the quality and the quantity of light which enters the leaf, and it operates to exclude completely the saturation deficit of the air as a factor in removing water-vapor from the leaf-surface, and thus in modifying the rate of gaseous movements in the intercellular leaf-spaces. The acidity of the guard-cells of the stomata may be changed through the modification of the light which strikes them and an alteration of their capacity for the absorption or excretion of water may follow in its wake.¹ The effect of the clips is apparently cumulative and the direction of the reactions are not easily or quickly changed.

The average indices of the course of the transpiring power are given in table 29, and are graphically shown in figures 9, 10, and 11. Although the transpiring power was not studied to any extent during the hours of darkness, the curves suggest the possible daily course. For

TABLE 29.—Average indices showing the daily course of the transpiring power.

	6 to 8 h.	8 to 10 h.	10 to 12 h.	12 to 2 h.	2 to 4 h.	4 to 6 h.	6 to 8 h.	8 to 10 h.
Aloe schlechteri...	0.106	0.098	0.032			0.024		
Aloe striata.....	.052	.020	.011	0.014		.012		
Cotyledon coruscans.....	.013	.009	.008	.022	0.009	.012	0.012	0.016
Cotyledon paniculata.....	.029	.013	.010		.008	.010	.012	
Eucalyptus globulus?.....	.082	.058	.170		.143	.155		
Euclea undulata...						.049		
Euryops lateriflorus.....	.133	.039	.032		.023	.030	.015	
Gasteria disticha..	.070	.052	.022	.019		.010		
Grewia cana.....	.120	.213	.145		.207	.115		
Gymnosporia buxifolia.....	.106	.111	.212	.125	.081			
Massonia latifolia..	.017	.067	.099		.094	.069		
Protea neriifolia...			.333		.305			
Rhus viminalis....	.132	.194				.101		

succulents the highest index is apparently at night or early morning. It falls early in the forenoon and is least at about midday or early afternoon. In the case of the sclerophylls, the highest index of transpiring power is apparently early in the morning, although in the case of *Grewia* it is also high in midafternoon. In *Euryops* it is highest at about sunrise, when it falls quickly. The possibly daily increase in the transpiring power of succulents at night, and the general daily course of the index for sclerophylls, appear to be similar to analogous forms as determined in America.²

A striking feature of the transpiring power of the species studied is the low maximum as well as the low minimum. The highest maxi-

¹ Physiology of stomata of *Rumex patientia*. J. D. Sayer. Science, vol. 57, p. 205, 1923.
² See references in Die Transpiration der Pflanzen, Burgerstein, 2 Th., 1920.

mum index was 0.472, for *Protea neriifolia*, which is not greatly above that of xerophytes, according to Bakke.¹ The highest for Karroo plants proper was 0.378, which was noted in *Rhus viminalis*. On the other hand, the maximum as determined might be extremely low, as, for example, was found to be the case in *Cotyledon coruscans*, where it was determined to be 0.016.

A very low minimum was found in the succulents, especially in *Cotyledon coruscans*, where almost failure of transpiration was demonstrated. The ratio between maximum and minimum indices in *C. paniculata* was found to be 106:1, as opposed to between 3 and 10 to 1 as in most of the cases noted.

The tests during one morning on the transpiring power of *Bauhinia marlothii* and *Welwitschia mirabilis* indicated that although growing under extremely arid conditions, both species have surprisingly high transpiration power. Further, the fairly high indices, for plants in a so arid region, were of the type characteristic of species without water-balance, or at least of sclerophylls rather than of succulents. This conclusion is advanced tentatively, inasmuch as further observations must needs be made in order to definitely establish it.

GENERALIZED SUMMARY.

In the main part of this paper summaries have been prepared for each subhead, and to such the reader is referred for summarized details of particular subjects. It is proposed, as to the few following paragraphs, to present some more general features relative to both the environment and to the plants, in which the general student of the arid portions of southern Africa may find interest.

The latitudinal situation of the regions of the subcontinent in which there is little rain corresponds fairly well to similar regions of Australia and of South America. Thus the latitude of Lake Eyre of South Australia is about that of the Central and Upper Karroos and of the southern extension of the arid region of the extreme west. Thus the situation of the arid regions in the south temperate zone is such as to place them under the influence both of the southeast trades and of the prevailing westerlies, with important resulting effects on the seasonal distribution of the rainfall. Such influences, however, are modified by others in southern Africa, to which the general climate owes much of its character. Thus there is the relation to the seas and to the general relief which are also most important. To the former is due the drop towards the south of the isothermal lines leading westward, as well as the fairly low temperatures of the north. And there are direct effects on the precipitation as well. Thus the air above the warm equatorial ocean current which is

¹ Studies on the transpiring power of plants, as indicated by the method of standardized hygrometric paper. A. L. Bakke. Journ. Ecology, vol. 2, 1914.

off the east shore is heavily moisture-laden as it drifts over the land in summer, bringing rains not only to the mountains and the plateaus near the coast, but into the far interior as well, and reaching even into Southwest Africa. In general, such precipitation decreases toward the west and may be little in the interior valleys, which are in the rain-shadow of the mountains. Along the western shore, on the other hand, the ocean current is from the south, so that the cold air above it holds relatively small amount of vapor. In the extreme southwest there are copious rains in winter, but in lower latitudes or the interior the winters are fairly rainless. Between the regions of summer and of winter rains, in southern Africa and also in Australia, lies an intermediate belt where the rainfall is at once uncertain, not only as to seasonal distribution, but also as to amount. This is the arid belt, extending in a general southwest-southeast direction, in which are to be found the Karroos, as well as the Namaqualands, and in the latter is included the Namib, the most arid portion of the subcontinent. But in much of the Karroo province, especially the eastern portion, the most of the rain is in the warm seasons. The seasonal distribution of the rain is of importance from the fact that the rainless seasons, having unlike temperature relations, have corresponding unequal values as regards the evaporation. As environmental factors, such conditions have well-recognized vegetational effects. Where the dry periods correspond with the seasons of higher temperatures, the perennial flora is markedly sclerophytic; chaparral or macchia is characteristic of the Cape. But where the dry period is in the cool seasons, other plant types prevail, along which are those typical of the Karroos, succulents, generally of small stature. In this instance, however, as will be commented on later, the causal relation may lie rather with the coincidence of sufficient moisture and appropriate temperatures. So far as the actual amount of precipitation in the drier portions of southern Africa is concerned, it can be said to range from less than 1 inch in the western Namib to about 15 inches in the lesser Karroos and in the eastern portion of the Central Karroo. Not all of the precipitation, however, finds its way to the water reservoirs of the ground or is of more direct use to plants. So, for example, a large rainfall within a short time may be mostly lost by run-off; and, on the other hand, an amount of rain so small as not to enter the soil appreciably is of little direct benefit. Such non-effective rainfall is usually relatively large in amount where the rainfall is little and thus may be an environmental feature of importance. Non-effective rainfall is defined as being less than 0.15 inch, occurring in a single stormy period. For several stations examined in this particular, it was found that the mean annual non-effective precipitation varied from 6 to 16 per cent of the entire amount recorded. The maximum was found to be 29 per cent. Fairly high percentages of non-effective rainfall are charac-

teristic for stations in the Karroos. The percentages of non-effective rainfall given above are, however, not especially high. Somewhat higher maximum non-effective precipitation has been determined for the Lake Eyre region, South Australia, for example, where so much as 43 per cent of the rainfall of one year should be so classed.

In portions of southern Africa where the summer type of rainfall prevails, the seasonal course of evaporation varies relatively little, and the largest amount may be in spring, or at least other than in summer; but where the rains are in winter the evaporation is not only relatively large, but it is also more variable as between seasons. In this case that of summer is the most. In order to somewhat more closely determine the evaporation at certain representative stations, atmometry was introduced in southern Africa. Although the preliminary results are not sufficient for generalization, they, however, indicate something of the possibilities of studying evaporation in southern Africa in this manner. A convenient and useful means of expressing aridity is to find the ratio between the amount of rainfall for a given period and divide this by the amount of evaporation for the same period. This is the index of aridity and gives a ready method of comparing the aridity of different stations as well as the seasonal variation at one and the same station, and has been much employed in other countries for these purposes. Mention has already been made of the relatively high evaporation-rate in summer at stations where the rains occur in winter. An illustration is afforded by the results at the National Botanic Gardens near Cape Town. In 1921-22 the following indices were obtained for winter and summer, respectively, namely: 0.0403 and 0.0005. As to differences when shorter time periods are concerned, the results at Irene are of interest. At this station having summer rains, the July index was found to be 0.0007, while that of the following October (midspring) was 0.0038. Finally, extremely low ratios were obtained in summer where there were no rains, as in portions of the Central Karroo. At Matjesfontein, in January 1922, for example, the index was 0.000016! An attempt, which was wrecked by miscreants, was made to determine the relative aridity of different faces of a kopje in the Karroo. Comparative results showed, however, that the northern face of the kopje was markedly more arid, as revealed by the atmometer, than the face opposite, and this conclusion was carried out by the observed differences in the flora. With the systematic study of evaporation as shown by the atmometer, which is in progress in southern Africa, observations of this kind will be greatly multiplied and evaporation as an ecological factor in southern Africa will be more thoroughly defined than is possible at present.

In traversing the regions with marked alterations of rainless and of rainy periods, or the intermediate regions where the rainfall is little and irregular as to time, the visitor sees a great variety of perennial

vegetation, even in the arid and semi-arid Karroos and in the regions north and northwest. Except along the streamways in the Karroos, in the savannah-forest west of Windhoek in Southwest Africa, and in the vicinity of Messina in the Low Veld, the writer encountered few trees, that is to say, in regions such as are especially considered in this paper. For the most part, the perennials that attract attention are small shrubs, but the variety of these is surprising. It may, very possibly, convey a right impression if one should state that toward the region of winter rains sclerophylls appear to dominate, with little suggestion of either deciduous types or of those that are succulent; that in the intermediate region, especially the Karroos, small succulents compose an important proportion of the perennial flora; but that where the summer rains prevail shrubs are not so abundant; here grasses come in, and in certain areas of large rainfall there are succulents of large size. In the Karroos and in the region of predominant summer rains, both deciduous and evergreen types are to be found. However, to give an adequate characterization of the flora in relation to the rainfall regions beyond, such general statements may not here be possible, and is at least not necessary for the present purposes. A leading point to be made is that there are tendencies toward one or another type of development, but that as a whole the result is very confusing. This is possibly to be expected from the very wide extent of the dry habitats. *Mesembryanthemum spinosum*, with small but fleshy leaves and with small spines, is an example of this mixed type of development. The character of the roots of this species (plate 26), which are essentially superficial, indicate that it should probably be classed among the succulents. As indicated in figure 7, they extend far in an east-west direction and are closely connected, on the east and south, with regions which also have a diverse climate, but one in which the rainfall is good. According to the work of Bews and of others, the relationship of the mesophytic flora of the latter regions and that of the flora of the dry habitats is close. This feature has possibilities which will be commented on in another connection below, but in this place I wish merely to point to the fact of climatic diversity, with especial regard to the dry habitats, and the further and presumably related fact of diversity in flora. Not all of these conditions of climate and of flora are sharply cut. There is more or less inter-relationship and dovetailing in both particulars. Thus, it is to be noted that in portions of the Karroos there is some rainfall in summer, although there may also be winter rains.

It does not appear to be unlikely, from what is known of the dependency of succulents on rains during the warm seasons, that the presence in the Karroos of plants of this type is to be traced immediately to the rainfall of the warm seasons. Where the summer rains are copious

the species with water-balance may be of large size. Thus, one may meet large *Euphorbias* with arboreal habit of growth (plate 5c), or shrubs with much shortened and bulb-like stems which rest wholly on the surface of the ground (plate 6c), or trees with massive stems and branches (plate 5A, 5B) which may perhaps be rightly classed with species having water-storage capacity. In the dry habitats, however, where the rains of summer are not so abundant, the succulents are usually not large, but yet they are extremely diverse as to growth-forms. It will suffice to point to those that are cushion-shaped (plate 11), others which are very small (plate 29B), and to the leaf succulents of different form and size (plates 11, 17, and 18), as well as to such stem succulents as certain *Euphorbias* (plates 8B; 13; 25c), and to the boterboom, *Cotyledon paniculata* (plate 18). The species last given is of particular interest in that it not only is the largest succulent of the Karroos, but that it occurs typically in regions having relatively good rainfall, of which much is in winter. It appears, however, that the species is vegetatively active during the fall and winter and that in late spring and in summer the leaves drop away, leaving the photosynthetic activities to be carried on by the green and fleshy branches. During the warm season, also, the boterboom produces flowers and fruits. The species appears from this to be vegetatively reactive to rather low temperatures. Even so it may be questioned whether without the rains of summer it would renew growth so actively in spring. The roots are superficially placed, as is the rule in plants of this class, and, for this as the leading reason, their growth may require fairly warm soil, as well as one with a suitable amount of moisture. But the temperature of spring probably meets this requirement. Further than this, the transpiring power of the leaves of the boterboom is relatively high, so that with no more adequate regulatory mechanism of this function than they appear to possess, the plant would not withstand the high evaporation-rates of summer without injury. There does not appear, however, to be any reason to suppose that the roots may not be active in moist soil in summer, and that being capable of absorbing water, they may not supply the water needs of the species of that season.

Comment has been made to the effect that mucilages in plants are organized under relatively moist conditions, while cell-wall material is formed where the conditions are especially arid. These physiological circumstances probably represent tendencies in development and stand for very fundamental differences in metabolism. Thus, in dry regions, spininess is often a marked characteristic, with the physiological process referred to as the probable immediate cause, although the species may have fairly marked water requirements. *Acacia karroo* (plate 14) is most striking in this regard. But it is to be noted that

one and the same species may be at once succulent and also spiniferous, although the development in either direction can not be said to be extreme.

The non-succulents, both evergreen and deciduous, of the dry regions of southern Africa are likewise exceedingly various and present features of interest; and, in addition, such regions are also noteworthy for what they do not possess, but might be expected to possess of plants of such types, and also the absence of certain organs found in analogous regions elsewhere is at once curious and striking. Thus species of the genus *Acacia*, as well as of the Proteaceæ, which are to be found under conditions of relatively great aridity in South Australia, where they are either large shrubs or small trees, and where they may stray away from water-courses, are, in southern Africa, either wholly wanting in the dry regions or confined to the banks of streams or to bottoms adjacent to them. In both continents the Proteaceæ are evergreen, and in Australia the same is true of species of *Acacia*, which are numerous. However, in this genus the evergreen quality is occasioned, as is well known, by the development of phyllodia which vary greatly in size and in form, and such are wanting in the species of southern Africa. It is of little use to speculate as to the reasons for the absence in the one case and the presence in the other of species or structures. It can be pointed out, however, that in the phyllodium of such Australian species as *Acacia linophylla*, of the intensely arid region west of Lake Eyre, the proportion of living cells of the "leaves" is relatively small, and *per contra*, that of non-living material is relatively very great. Such being the case, the water requirement is small at all times and the species is in position to produce foods photosynthetically also at all times.

With the relatively small size of the phyllodia of this species and the small number on a plant, even of good size, it can be seen that it is wonderfully adjusted to an arid environment; and it is to be doubted whether species of the same size and habit of growth, but with deciduous leaves or leaflets, even small in size, would survive in the habitat referred to. Thus the tendency of species to organize anhydrides under conditions of aridity works in the direction of also better adjusting them for the unfavorable moisture relations of an arid habitat, and this largely by insuring not only protection for the living cells, of which many are engaged in carbon assimilation, but also probably to a certain degree extending the possibilities of water storage, as well as to bring about, indirectly to be sure, the fact that a relatively small proportion of the tissues can be said to be living.

In his rapid survey of the flora the writer failed to see aphyllous species of consequence, aside from the *Euphorbias*, although certain forms with green branches were seen to be without leaves in winter. It is possible, therefore, that aphyllly is not a common occurrence in

the arid habitat of southern Africa. The perennials do exhibit reduction in leaf-surface, however, in different ways and often in remarkable degree. In this respect, however, they were not especially different from analogous plants in other and similar dry habitats. Beyond the reduction of the external surface, especially of foliar organs, the possible means of cutting down excessive evaporation, by morphological means, were found to lie in the reduction of the size of the intercellular spaces, by which the internal evaporation surface is reduced, the frequent limitation in amount of the living tissues, whether chlorophyll-bearing or not, and the coating of the outer surface with waxy or resinous materials. So far as these features are concerned, comment need only be made of those last referred to. Frequently, possibly always, the secretion of wax or resin is of ecological significance. Thus in *Rhus viminalis*, which occurs by streams in the Karroo, the resinous secretion is slight, but in *Rhus* sp., which grows on low kopjes not far distant, the amount of secretion of this nature is very much greater and in fact is very considerable. When, however, it becomes excessively thick, as on the stems of species of *Sarcocaulon* is sometimes the case, it should possibly be regarded as a physiological condition and as such a direct reaction to the arid environment. It does not appear that the leaves of these plants are exceptionally heavily covered with resin, but only the stems. It should be remarked here that trichomes of various sorts are often found in young leaves, but less often in those that are mature. In such case the exposed surface may be greatly increased, but owing to the character of the trichomes they may, however, operate to shield the leaf against harmful effects of excessive illumination as well as against a dangerous rate of water-loss from the epidermal cells.

The perennials of such arid habitats as those of southern Africa often have roots which, in the direction of their development as well as in size and in other features, may be highly characteristic. Thus it appears that as a rule succulents have the type of root system in which none penetrate the ground deeply, not even excepting the anchoring roots. Those of non-succulents, on the other hand, may exhibit fairly wide diversity in this regard, and with respect to root development may be quite comparable to similar plants in dry habitats elsewhere. In certain species, as *Lycium* sp., where there are superficial roots as well as those which penetrate deeply, the nature of the soil permitting this, shoots may spring from those which lie close to the surface of the ground. How common such vegetative means of reproduction may be in southern Africa was not learned. In other arid regions, as, for example, in South Australia, it was found in several species, and it is also known to occur in semi-arid portions of southwestern United States. Owing to the inherent difficulties of becoming established in an arid habitat, many of which are overcome by such

means, it is rather surprising that it is not more commonly met. The effect will be seen to be somewhat different than the renewal of an individual through the upspringing of shoots at the bases of the stems or branches. In the former case new territory is invaded, while at the same time that previously occupied is yet retained.

Another feature which should be mentioned is the occurrence of slender rootlets in groups in the soil horizon most commonly wetted by the rains. These appear to be formed each season with the moistening of the soil and to dry up and die when the upper soil becomes impossibly dry. Such "deciduous" rootlets are seemingly peculiar to perennials of an arid habitat and appear not to be formed in more moist situations. Mention was made in the preceding paragraph to the effect that in succulents the roots are not deeply placed. The statement requires qualifying. The writer did not see the roots of the tree-like *Euphorbias*, which do not occur in the arid regions, but he supposes from analogy that they possess anchoring roots which provide a portion at least of the support of the plant and which may penetrate the ground to a certain depth. However, in the geophytic species, as *E. multiceps*, where anchorage of the sort referred to is not required, the root-system is dominated by a tap-root which reaches fairly deeply. In this case the root is highly specialized and of the obligate type. No superficial secondary roots of importance are organized. It is a striking exception to the rule for root formation in succulents.

The chlorophyll-bearing organs of perennials are the portions of the plant most directly affected by changes of whatever sort in the subaërial environment. In a dry habitat, such as the Karroos or the Namib, it is not surprising that the structure of such organs exhibit to a degree the results of the reaction of the leaf, for example, to the impinging environment, but it is of interest to note the presence in the foliar organs of useless (?) structures common to such members of the family as may be living under mesophytic conditions. By contrasting the essentials in the inner morphology of leaves of xerophytic and mesophytic members of the same family, it seems possible to arrive at the leading structural adjustments wrought in response to living in the arid habitat. This has been done tentatively and in a very limited way in the body of this paper, and need not be presented in detail in this place. Certain of the more interesting features, however, may be alluded to.

It is pointed out that the formation of a heavy outer epidermal wall occurs in all species where there is no covering of trichomes. It should be added that in the species studied the inner wall of the epidermis remained unthickened and that usually only the outer portion of the lateral walls increased in thickness, although prominent exceptions to the statement last made were met with. Such conditions

would be expected, in view of the circumstance that cell-wall material is actively organized in conditions of aridity to which it will be noted the outer epidermal wall of such species is always especially subject. The result has ecological importance, but the process is purely physiological and a teleological explanation is not fitting.

A frequent, but not universal character of the xerophytes examined was found to be deep placing of the stomata with respect to the general level of the leaf-surface; but this does not entail the development of a novel character, from the fact that it is apparently always through the formation of a heavy outer wall of the epidermis that the stomata come to have this position. It, however, was noted in certain species that there is a marked constriction of the entrance of the stomatal pit, which, in addition to the outer vestibule ridge, must operate to cut down the passage of gases. The epidermis was found to consist of only one layer of cells, except in three species, of which two only, and possibly only one, *Welwitschia*, can be said to be markedly eremophytic. As to other structures, it will suffice to remark that supporting tissue was not found so abundant in the foliar organs of southern Africa as in those of South Australia. As to the chlorenchyma, it need only be remarked that most of the species have palisades on both sides of the leaves, but many leaves are not isosymmetrical, but are dorsi-ventral in their structural symmetry. The last remark applies to the non-succulents. In succulents the outer chlorophyll-bearing cells are not pronounced palisades and those within are cuboid, but the chlorenchyma is apparently alike on both sides of the leaf.

The possible departures from structural features characteristic of mesophytic members of the families to which the species examined belong will be seen thus to be surprisingly few in number, although often striking when studied in detail. They consist very largely in relatively small modifications of the epidermis and of epidermal organs with a marked tendency, in non-succulents, to the formation of cell-wall material, as to the inner morphology, and in a reduction of the surface of the transpiring organs as well. Such divergences from the features of the mesophytic members of the family are of a consequence of the order of qualitative differences and are strikingly small when the intimate relationship of the leaf with the marked characteristics of the arid environment are taken into account. As to morphological relations of other portions of the plant, which are not here considered, even greater conservatism might be expected and probably may be found.

In a general way, there appears to exist a very definite relation between the ability of a xerophyte, and reference is here only made to those studied in this particular, to give off water-vapor and the aridity of the habitat and thus with the xerophytism of the species. Should it be possible to account for all the water received in the habitat, and

in every way, there might be little exception to this statement. Independent of this, however, it still is often true that the transpiring power of the leaves checks very closely with the character of the plant and with that of its environment. Thus such species as *Protea neriifolia*, which does venture away from fairly mesophytic conditions, appears to have a relatively high transpiring power, while that of *Gymnosporia buxifolia*, of the Karroo, is relatively low, to cite two examples. A very low index was determined for leaf succulents at Matjesfontein, in certain of which the fact of transpiration was on occasion determined with difficulty. Such forms were confined to low kopjes. On the other hand, species by the water-course showed fairly high indices of transpiring power. Regulatory adjustment, by means of which destructive loss of water is avoided, appeared to be the case in certain species in which the transpiring power was higher when the air was humid than when the relative humidity was low.

There thus seems to be a relationship between structure, physiological reactions, shoot and root development, and the local and general distribution of the species. As to the last, this paper has little to do. The botanists of South Africa are actively engaged in following out the distribution and possible origin of the flora, including that of the arid habitats, in an intense and well-organized manner. Some remarks, however, may not be out of place as regards the occurrence of species in such habitats as the writer had under observation, which are situated in the western part and the east-central part of the Central Karroo, and a small area of the Namib Desert.

The local distribution and occurrence of the woody plants have some features of interest. The larger species, as trees, may be present even in a desert district, but if so they are confined to water channels. The relative humidity of the air may be low, but if the roots are provided with an adequate supply of water a high rate of evaporation appears not to be inimical to many trees. But the lesser perennials have greater range in their distribution. Where, as on the Namib, the conditions of aridity are intense, shrubs are generally wanting and may only be found in shallow drainage channels, if on the higher plain, or by the main streamways. In somewhat better watered regions the shrubs creep out on the plain away from the water-courses of whatever kind. They are of good size and abundant if the ground-supply of water is fairly plentiful, or they may be of good size but scattering; or finally, they may be relatively small but still fairly abundant if soil or water conditions are not both relatively favorable.

The above remarks have to do with non-succulents more particularly. If succulents are present, and especially if they are not of large size, they are often gathered in numbers at the bases of the larger non-succulents, increasing the total population and even doubling it. Such distributional characteristics are often encountered in the

Central Karroo, together with others which need not be taken up in this paper.

The reactions and adjustment associated with the local distribution of the lesser perennials are probably sufficiently complex, and no attempt will be made to adequately account for them; but there are certain relationships which are apparently causal to which allusion may be made. Thus, to take up at first the condition last referred to, that is, the relationship of succulents and of non-succulents, it may be pointed out that the root-system of the former is necessarily meager and as a whole situated close to the surface of the ground, while that of the larger "protecting" form may be extensive and may penetrate the ground deeply, or fairly so. Such mutual accommodation decreases, if it does not wholly do away with, competition between the roots of the two types of plants for room and moisture. But the matter may not end here.

It seems possible that the succulent may possibly derive real protection from excessive light, or evaporation, by the association, or that there may otherwise be better moisture relations. It accordingly happens that in another habitat, where the water relations may be somewhat better, the same succulent may be found growing quite independently of larger forms. Where the conditions last named are not met, the two types of plants seem to be distributed with little relation to each other. When, however, either occurs alone, there is a certain adjustment by which the plants come to be fairly equally separated, and thus as between equal areas to have about the same population. So far as are concerned possible reasons for the correlation of size and numbers, it can be said that, other features being equal, the larger the size of the individuals, the fewer can occupy a given area. But under conditions which were not fully worked out, it appeared that in some areas where there is fairly intense aridity the shrubs are dwarfed, as might be expected, but at the same time they may be found to be very numerous. So anomalous a condition was found difficult to explain. It does not appear improbable, however, from what was observed of the behavior of such species, that the limitation in the amount of soil moisture worked to restrict both root and shoot development, with the effect that in such areas a fairly large population of dwarfed non-succulents is supported.

An examination into the local occurrence of species, with the necessarily somewhat close study of plant habits, impresses the observer along two opposite lines. On the one hand, there is often seen to be marked diversity among perennials as to habit of growth even in the same habitat, but on the other hand, species belonging to different genera, and even of different families, may be strikingly alike, although superficially so. In the circumstance last named the veld appears be populated with but a single species, of equal height and of the same

general appearance, when in fact monospecific communities do not appear to be common in the arid habitats of southern Africa. Whether rightly so or not, the observer is likely to be convinced that at least where the growth habit tends toward the uniform, there is manifest in the fact a direct adjustment to the various environmental factors based on physiological reactions. In the last analysis this attitude connotes a long period of time during which the adjustments are constantly taking place, and it may include gradual if slow environmental changes of the habitat itself, in this case moving away from the humid and terminating in the desertic, in which extreme the uniformity of habit characteristic of the mesoxerophytic habitat may be lost.

The possible leveling of plant habits in the intermediate stages between desert and mesophyllous conditions, such as are observed in the Central Karroo, for example, offer many features of interest. Thus among the marked characteristics of the flora, as above remarked, are often superficial resemblances of species of different genera, or even of different families. A few examples may be cited. At the outset there may be pointed out instances where certain species of the Karroo veld are similar to species of arid regions elsewhere. Thus *Euphorbia stellæspina* (plate 8) of the Central Karroo has a close resemblance to small species of *Cereus* of portions of southwestern United States. An inspection of the plate will reveal the presence of longitudinal furrows, as in *Cereus*, which can hardly fail to have a similar function, namely, that of accommodating the plant to a varying store of water, through which the tissues expand when turgid and contract on sufficient water-loss, without injury, and the general similarity between many other species of *Euphorbia* and of different species of the cacti is common knowledge. Also, the *Aloes* strongly recall species of *Agave* in the fact of a common leaf succulence. And the arborescent *Aloe dichotoma* on the plains of the Southwest Africa has many points of resemblance with *Yucca arborescens* of the Mojave. Not to extend the list, it can be mentioned that species of *Sarcocaulon* may be very like young *Fouquieria splendens*. The resemblance last referred to extends in certain species to the deposition of wax or other material in the cortex. So far as conditions on the veld are concerned, it will be understood that there may be both marked uniformity as between species of a single genus and marked diversity as well. While nearly any genus may be cited to support this, it is preeminently the case in *Mesembryanthemum*, as is well known. Referring to the frequent tendency of species of different genera or families to have a similar vegetative expression, one can mention species of *Crassula* and of *Cotyledon*, which are sometimes so nearly alike that only close inspection will reveal the identity of each. Also, the resemblances between species of *Senecio* (plate 10) and *Euphorbia* (plate 13), although not

close, are, however, quite evident. Mention can also be made of *Stapelia* (plate 28D), which recalls certain species of *Euphorbia* and certain cacti as well; and, too, there is also a likeness between cushion forms of *Cotyledon* and of *Mesembryanthemum* (plate 11). By including the non-succulent types, the list of resemblances in plant types might be much extended. Something of the uniform character of much of the flora of the veld is shown in plates 6A, 6B, 12.

With such leveling processes active, one can well understand how in course of time there may result a certain degree of floral monotony as to perennial woody species, such, for example, as is characteristic of much of the landscape of South Australia. It will be seen that such result may be other than, and quite distinct from, the occurrence of one species only in a single habitat, the aspect of which would be the same.

The physiological reactions associated with such vegetative modeling as has been referred to are various and complex, affecting both the root and the shoot. It has already been shown that possible differences in capacity for excretion of watery vapor, as between unlike species, is of importance in the sorting-out process by which each comes to live in the habitat having an appropriate water-supply. A low capacity may signify possible survival in an arid habitat. Differences in the total requirement of water also operate toward the same end, that is, toward the adjustment of species to the habitat and to each other. A great moisture deficit of the air occasions a rapid rate of evaporation, so that water taken in by the roots is divided during growth as to its ultimate physiological fate, a relatively large amount leaving the surface of the shoot in transpiration in proportion to that fixed in the metabolic processes. Such partial starvation restricts shoot growth in all ways, but particularly as regards the distal members, or foliar organs, which are most intimately affected by the sub-aerial environment. Short shoots and small leaves are a consequence of this group of reactions. There are also immediate structural effects which should be noted. Owing to the fact that under conditions of aridity anhydrides are recognized, the cell-walls of xerophytes may be heavy. This remark applies to the outer epidermal wall in all instances, except when there is a cover of trichomes, and, to a less degree, it is true, several other tissues of the leaf. With the increase in the thickness of cell-walls there is a corresponding decrease in the living cell-contents, and this directly operates to cut down the water requirements of the species.

Such remarks, it should be noted, apply to non-succulents, especially to xerophyllous sclerophytes, of which the foliar organs are not only small but relatively thick as well. As to succulents, it has been determined that under more moist conditions mucilages, with high water-absorption capacity, and not anhydrides, tend to be formed.

The permanent foliar organs of plants of this type appear usually, or always when mature, to have low capacity for moisture excretion, and in possible association with this circumstance the roots are usually meagerly developed and lie close to the surface of the ground.

Finally, a word should be said in regard to the reaction of the roots of xerophytic species of different growth habit. In certain succulents it has been found that a relatively high soil temperature is requisite for an adequate rate of growth, and since in all species an appropriate supply of moisture in the soil is a prerequisite for growth, it accordingly may happen that succulents occur most extensively, or only, in regions with rains in summer. But so far as the root-systems of non-succulents are concerned, the matter is otherwise. There are in such forms, as in succulents, specific adjustments to the temperature of the soil, which may in these forms include low temperatures, of which one result is the characteristic placing of the roots. The differences in the reaction of roots to the temperature of the soil, as, for example, in slopes with unlike aspect, may be an important factor in determining the local distribution of the species. The possible differences in the reactions of roots of diverse species to the oxygen-supply of the soil is another condition of much importance; and this has relation to the temperature at which the root best grows, and may be specific.

Not to further extend the list of reactions of a species of the arid habitats, it will be appreciated that they are immediately concerned not only with the major environmental factors, of which but a few have been alluded to, but with minor factors as well, and the important point is that the unlike species react to such common impinging environmental factors. Where reactions take fairly parallel courses, the results are to a certain degree harmonious, and to the degree that they are so the species tend to become more and more alike. Thus, as earlier remarked, it is not difficult to appreciate how in an arid region there may be similarity between the vegetative parts of different species and how by the association of those with most harmonious reactions there may be formed a flora with superficially similar individuals, and which may thus be fairly monotonous, or how, where there are fundamental differences between species as regarding metabolic processes, as between succulents and non-succulents to cite extreme types, there may be floral diversity. Such are the logical and inevitable results of physiological reactions of the living forms to so pronounced an environment as that of the arid portions of southern Africa.

A word should be said in conclusion regarding the combination of experimental and of observational work in general studies on plants. It needs no argument to support the statement that only so far as the reactions of plants to such factors as temperature, moisture, oxygen, and the chemical and physical conditions of the soil, are studied can the

possible adjustment to an environment possessing these factors be reasonably well known; and, in order to apply the results of such studies as much as possible should be known in regard to the environment itself, which again is self-evident. Such physical and physiological investigations are particularly desirable in association with an arid habitat, where the relations are largely between the plants and the habitat, rather than importantly between the plants themselves.

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A. *Welwitschia mirabilis* showing character of habitat, about 40 km. east of Swakopmund, looking toward the Swakop River.
B. *Acanthosicyos horrida* in bottoms of the Swakop River, 15 km. east of Swakopmund.

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A. *Welwitschia mirabilis*, Namib Desert, about 40 km. east of Swakopmund. Female plant.
B. *Welwitschia mirabilis*, habitat of A. Male plant.
C. *Zygophyllum stapfii*, leaves, natural size.

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- A. Vegetation in *Welwitschia* habitat, about 50 km. east of Swakopmund, Namib Desert. *Asclepias filiformis* (left), *Zygophyllum stapfii*, and *Bauhinia marlothii*. Looking south.
- B. Vegetation in *Welwitschia* habitat. Looking north, toward the Swakop River. The dark shrub-lets are *Zygophyllum stapfii*. *Asclepias filiformis* (?) is in the bottom of the shallow wash.
- C. *Zygophyllum stapfii* in habitat of *Welwitschia mirabilis*, about 40 km. east of Swakopmund, Protectorate of Southwest Africa.

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A

B

A. *Arthræua leubnitzii*, about 18 km. east of Swakopmund, Namib Desert. Plain south of the Swakop River.
B. Branch, natural size, of *Arthræua leubnitzii*.

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- A. Tree type in Low veld, near Messina, northern Transvaal, rainfall about 25 inches, of which about 90 per cent is in summer. *Sesamnothamnus lugardii* (?).
- B. *Adansonia digitata*, near Messina, northern Transvaal, July, showing enormous development of stem which constitutes a water-storage organ of great capacity. Rainfall about 25 inches, of which about 90 per cent is in summer.
- C. *Euphorbia cooperi* by the Zoutpansbergen, rainfall 35 inches, or over, of which about 90 per cent occurs in summer.

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- A. View of veld, looking southwest from kopje near Beaufort West, central Karroo.
B. South face of doleritic kopje, near Beaufort West, Central Karroo.
C. Bulboid squat stem of *Adenia schlechteri*, resting freely on surface of ground, with water-storage capacity. Low veld near Messina, northern Transvaal. Rainfall about 25 inches, 90 per cent in summer.

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- A. *Gymnosporia buxifolia* (?) on kopje near Beaufort West. Used in transpiration studies.
- B. Branch with leaves, half natural size. *Grewia cana*, from kopje near Beaufort West. Used in transpiration studies.
- C. Leaves and spines of *Gymnosporia buxifolia* (?), one-half natural size. From kopje near Beaufort West, Central Karroo.

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- A. *Aloe schlechteri* on north slope of kopje near Beaufort West.
B. *Euphorbia stellaespina* on north slope of kopje, near Beaufort West.
C. Quadrat No. 1, on south slope of kopje (compare plate 6B), near Beaufort West. The following are included among the perennials occurring in the area: *Carissa ferox* (?), *Euphorbia mauritanica*, *Grewia cana*, *Lycium* sp., and *Mesembryanthemum* sp.

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A. *Gasteria disticha* growing at base of *Euphorbia mauritanica* (?) on upper south slope of kopje near Beaufort West. Used in transpiration studies.

B. *Massonia latifolia* at base of *Lycium* sp. on slope of kopje near Beaufort West. Used in transpiration studies.

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A. *Crassula quadrangularis* growing at base of *Lycium* sp. on upper face of kopje near Beaufort West.
B. *Senecio longifolius*, by water-hole, 6 miles east of Beaufort West.

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A. *Cotyledon decussata* growing at base of *Lycium* sp., Prince Albert Road, Central Karroo.
B. *Mesembryanthemum calamiforme*-*Cotyledon hemisphaerica* (?) community, Prince Albert Road, Central Karroo. Rainfall 4.57 inches; 60 per cent in summer.

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- A. Quadrat No. 3, near Matjesfontein, looking toward the Wittebergen. There were 330 individuals, perennials, on the area, 10 by 10 meters, about equally divided between succulents and sclerophylls.
- B. Veld near Matjesfontein, looking toward Ngaap kopje. *Mesembryanthemum spinosum*, M. spp., *Pentzia virgata* dominate.

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A. *Euphorbia mauritanica*, veld near Matjesfontein.
B. *Euphorbia eustacei*, among rocks, near Matjesfontein.

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A. *Acacia karroo*, in winter (August), near Matjesfontein.

B. Detail of A showing marked spiniferous character of branches, which is especially noticeable during the leafless condition.

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A. *Mesembryanthemum junceum*, on veld near Matjesfontein.
 B. *Euryops lateriflorus* by rocky outcrop near streamway, Matjesfontein. Used in transpiration studies.

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A. *Cotyledon wallichii* on low kopje near Matjesfontein.

B. The leaf succulent *Cotyledon coruscans* on slope of low kopje near Matjesfontein. In flower.
One specimen of *C. paniculata*, stem succulent, is shown in middle ground at left.

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A. *Crassula perfoffa* with *Cotyledon orbiculata* at back; *Grewia cana* at left. Kopje near Matjesfontein.
 B. Vegetation on north slope of kopje, near Matjesfontein. *Euphorbia mauritanica* in middle foreground, with *Cotyledon orbiculata* at left in middle ground; *Aloe striata* (?) in middle ground and background. *Mesembryanthemum spinosum* and *Crassula perfoffa* dominating. *Grewia cana* and *Lycium* sp. at left and right in background.

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A. *Cotyledon wallichii* on veld near Matjesfontein.
 B. *Cotyledon paniculata*, stem succulent, on kopje near Matjesfontein, *Mesembryanthemum junceum* (?) dominating.

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A. *Protea neriifolia* at Tweedside, west of Matjesfontein, used in transpiration studies.

B. Vegetation of kopje, near Matjesfontein. *Mesembryanthemum junceum* in flower in middleground; *Aloe striata* (?) with flowering stalks on either side. Small specimens of *Cotyledon paniculata* at right in foreground and at left in middle ground. *Euphorbia mauritanica* in right middle ground with *Euclea undulata* behind.

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A. Streamway vegetation, near Matjesfontein. *Rhus viminalis*, in middle ground, with *Acacia karroo*, in front, as a shrub, and on the left as trees.
B. *Lebeckia psiloloba* on edge of village, Matjesfontein. It occurs in some numbers on kopjes a few miles west.

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- A. General view of quadrat No. 4, near Matjesfontein. *Mesembryanthemum spinosum* and *Pentzia virgata* dominant. *Asparagus capensis*. Out of 397 individuals, perennials, 184 are succulents.
- B. Vegetation on lower slope of foothills near Whitehill, 3 miles east of Matjesfontein, Central Karroo. *Euphorbia mauritanica*, left foreground; *Crassula portulacea*, middle ground; *Asparagus* sp., *Rhus* sp., and *Euclea undulata*.

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A. Root exposure of *Galenia africana* (left) and *Erioccephalos*, showing characteristic deep penetration in both species, with prominent development of superficial roots in the latter. Matjesfontein, near streamway.

B. *Euphorbia stolonifera* on rocky portion of veld, near Matjesfontein.

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- A. Prominent development of superficial roots in *Asparagus* sp. on veld near Matjesfontein. *Mesembryanthemum spinosum* at left and immediately back of the small *Asparagus* shoot.
- B. Root exposure of *Euryops lateriflorus* by small wash, 7 miles west of Matjesfontein. The small shrubs in the background are in part *Galenia africana*.

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- A. Superficial and fairly meager root system of *Euphorbia stolonifera* exposed in part by erosion, with *Cotyledon* (?) in shadow, and *Mesembryanthemum spinosum* in background.
- B. Exposure of roots of *Cotyledon canescens* by small wash near Matjesfontein. There were two main roots, both superficial, with numerous short roots. One of the main roots lies on the surface of the ground in the foreground, and the other is to be seen in front of a sheet of paper back of the plant.
- C. Root system, removed soil, of *Cotyledon coruscans*, showing its meager development. The roots are mainly superficial. Veld near Matjesfontein.

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A. *Euphorbia multiceps* showing prominently developed tap root; veld at Matjesfontein.
B. *Euphorbia multiceps*; veld at Matjesfontein.
C. *Aloe variegata* in flower; veld near Matjesfontein.

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- A. Root system of *Mesembryanthemum junceum* showing prominently developed superficial roots. About one-third natural size. Veld, near Matjesfontein.
- B. *Mesembryanthemum spinosum* showing characteristically marked development of superficial roots. Flats south of Whitehill, 3 miles east of Matjesfontein.

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- A. *Elytropappus rhinocerotis*, near streamway, Matjesfontein, showing prominently developed superficial roots, of the generalized root system, exposed by erosion.
- B. Root exposure in *Lycium* sp. growing by stream near Matjesfontein, showing vegetative reproduction from superficial lateral, and strongly developed tap-root.

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- A. *Anacampseros papyracea*, one-half natural size, Whitehall, 3 miles east of Matjesfontein.
B. *Androcymbium* sp., one-half natural size, veld at Matjesfontein.
C. *Crassula columnaris* in right middle ground, in flower, and in preflowering stage.
Mesembryanthemum pygmaeum (?) at left. About one-fourth natural size, veld at Matjesfontein.
D. *Stapelia pillansii* on low outcrop near Matjesfontein.

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A. *Haworthia* sp. showing the fleshy and short superficial roots; veld, Matjesfontein, natural size.
 B. *Mesembryanthemum pygmaeum*, left; young *Crassula columnaris*, below; *Cotyledon* (?), right.
 Two-fifths natural size.

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A. Young plants of *Cotyledon paniculata*, natural size, showing early development of succulency in the stem; veld, near Matjesfontein.
B. *Crassula lycopodioides*; veld, near Matjesfontein. Natural size.

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- A. Young plant, one-half natural size, of *Cotyledon wallichii*, showing the early development of succulency in the stem and superficial nature of meager root system; veld, near Matjesfontein.
- B. *Pelargonium crithmifolium* showing prominent development of tap root one-half natural size; veld, near Matjesfontein.

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