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AN ACCOUNT OF THE CHIEF TYPES OF VEGETATION IN SOUTH AFRICA, WITH NOTES ON THE PLANT SUCCESSION

By J. W. BEWS

(*With one Figure in the Text*)

INTRODUCTION

It seems to be an unfortunate necessity for any writer, who uses the term "formation" in connection with the study of vegetation to endeavour to define what he means by it. Plant Ecologists, however, are fairly well agreed that the term "formation" should be applied to certain natural units of the vegetation. The difference lies in the methods of determining the units. Most of the European continental ecologists including Schimper (**22**), Warming (**30**) and Drude (**12**), use "formation" to express definite physiognomic types. The British ecologists (**28**), on the other hand, emphasize the habitat as determining the formation. Since the climate of the British Isles is relatively uniform, habitat comes to be mainly a question of soil conditions and soil therefore is the master factor adhered to by the British ecologists in their system of classification. This is perfectly justifiable and in fact necessary where the climatic factors are more or less uniform.

In South Africa, however, climate is on the whole more variable than soil conditions though they both vary. To use soil as a basis of classification for South African vegetation would hardly succeed. Even in small areas climate is more important, as for instance in the Cape Peninsula, that wonderful botanical area which though only 197 square miles in extent, or a little larger than the Isle of Wight, yet, according to Bolus and Wolley-Dod's list (**6**) has no fewer than 2117 species of flowering plants. The one side of Table Mountain has Bush of the Eastern type, the other side sclerophyllous heath and Macchia. This striking difference is here certainly not due to soil conditions but to the marked difference in climate due to the S.E. mist and rain clouds. Bolus states that the annual rainfall for an average period of ten years varies between 21 and 28 inches for various stations on the N.W. side, while on the S.E. side it varies between 43 and 63 inches.

Again at Knysna no difference can be detected in the type of forest which covers the two geological formations, the Bokkeveld and Table Mountain Sandstone. In Natal, every mountain from the coast to the Drakensberg has a distinct type of vegetation on its two opposite slopes (southeastern and northwestern), depending again solely on climatic differences. The valley vegetation, too, differs from that of the higher levels, a difference however in this case depending partly on climate, partly on soil. The edaphic factors, therefore, must be recognised when necessary but the basis of any system which can apply to South Africa must be climatic. This has clearly been recognised from the first and South Africa has accordingly been divided into various botanical regions by Drege, Grisebach, Rehmen, Engler, Drude, Bolus and Marloth (15). The last mentioned author has given a series of maps illustrating the historical development of this part of the subject. The climatic factor chosen has been rainfall, but it is chiefly the floristic differences in the various regions that have hitherto been dealt with.

If we use the climatic factors as the basis of our system of classification, it becomes to a large extent physiognomic, for physiognomy is determined much more by climate than by soil conditions. At the same time, the British school have done well to emphasize the importance of habitat, though it is not only the edaphic habitat but the climatic that we have to recognise in South Africa.

At the present state of our knowledge, the units recognised as formations in South Africa are very large. Each of them has its own climatic habitat but it is not absolutely uniform nor are the types themselves. As our knowledge increases, the number of formations will also be increased. For instance I have included all the grassland without trees in one large formation, the Veld. At the same time, in former papers dealing with Natal (1, 2) I have described two very distinct types of it, High Veld and Low Veld, which, though the same species, *Anthistiria imberbis*, happens to be dominant in both, yet differ in climate, soil conditions and even in physiognomy. There are many others as distinct, e.g. the Tussock Veld of the mountain regions (3) as well as the Veld of widely separated geographical areas, such as the western region, where the toa-grass, *Aristida brevifolius*, grows in isolated tufts on the great sandy plains. All these may perfectly well be considered separate formations. Veld will then become a formation group or vegetation type. At present, however, while we are endeavouring to obtain a general, clear impression or bird's eye view of the vegetation as a whole, it is better not to enter into too great subdivision.

Cowles (9) defined three cycles of vegetative succession, as follows. (1) Regional successions "due to secular change and, in rate of development, bearing some comparison with the succession of geological periods." In South Africa, as in other countries, there has been a certain amount of more or less speculative writing on this subject but I do not propose discussing it

in the present paper. We have nothing quite so straightforward to deal with as, for instance, the post-glacial changes in the vegetation seen in North Europe and America. (2) Topographic successions "of much greater rapidity and associated with the topographical changes resulting from the activities of such agents as running water, wind, ice, gravity and vulcanism and leading generally to erosion and deposition." South Africa is an ideal country for the study of this type of succession. Where the rainfall is sufficient, as in Natal, denudation is going on with extreme rapidity and there is also rapid accumulation of deposits in certain places. The former leads to retrogression in existing stable types and the latter to progressive changes. (3) Biotic successions, where the changes are due to plant and animal agencies. "The influence of biotic agencies is not confined to areas that are characterised by a pre-erosion topography, because the interval between the periods of active erosion often is sufficiently long to permit the development of an entire biotic cycle."

Other American writers and notably Clements (7, 8) have given attention to succession. Clements has laid down certain laws of succession and the following summary gives his more important conclusions. (1) A succession results from the appearance of a new habitat or a striking change in an existing one. (2) Each stage of a succession reacts on the habitat so as to produce conditions more or less unfavourable to itself but favourable to the invaders of the next stage. (3) Initial formations are open: ultimate formations are closed. (4) The universal tendency of vegetation is towards stabilization. (5) The ultimate stage of a succession is determined by the dominant vegetation of the region. Lichen formations are often final in polar and nival zones. Grassland is the final vegetation for plains and alpine stretches and for much prairie while forest is the last stage for all mesophytic habitats. (6) The end of a succession is largely brought about by the progressive increase and competition, which makes the entrance of invaders more and more difficult.

The term "formation" is applied by Clements to stages in the plant succession. Crampton (10, 11) emphasizes the influences of the geological agents of surface change and distinguished two classes of plant formations, "Stable" and "Migratory." "The plant associations of stable formations are stabilized to the extent allowed by the prevailing climate and edaphic conditions, and are of long persistence on the same habitat, but their boundaries are subject to frequent retraction and expansion owing to the migratory nature of the habitats of the migratory formations." Stable formations resist invasion as long as climate and geographical conditions remain unchanged. In open stable formations, the physical conditions limit invasion. Migratory formations "are of comparatively short persistence on the same habitat which sooner or later undergoes change or destruction with renewal elsewhere." All the writers who have approached the subject from

this standpoint agree in seeking for causes in the geological changes, whether of major or minor character, but in addition and to a large extent dependent on the geological changes, we have climate variations often quite local and at the same time fairly extreme and in South Africa these are of considerable importance. It is this aspect of the subject which will of necessity be emphasized in this contribution.

It is, of course, quite impossible to deal exhaustively with the plant succession in a short paper such as this, and much further study will be necessary before the facts are at all adequately known. What is offered must be considered merely as tentative suggestions which may be modified and will certainly be amplified by further research. As far as Natal is concerned, details of the composition of the various plant associations referred to have been published elsewhere (1-4) and for the rest, various other works have been consulted to amplify the knowledge gained as the result of short visits paid to various parts of the sub-continent.

THE SUCCESSION ON BARE ROCK-SURFACES AND CLIFFS

A. **Lithophyte Succession.** In Natal, seeing that the rate of denudation is very great, there is a large development of cliffs, particularly in the Drakensberg range, where they are often several thousand feet high. There are, however, no sea-cliffs and one type of succession, therefore, common on rocky shores is eliminated. On the inland cliffs, the plant succession has only been investigated in a few localities, but probably the succession found there is more or less characteristic of them all, though of course it is to be expected that numerous minor variations will be found to occur.

The plant associations appear in the following order.

(1) *Associations of Cyanophyceae.* On the Drakensberg cliffs at the Goodoo Pass, the earliest colonist is a blue-green alga, *Glæocapsa sanguinea* Kütz. This is quickly followed by two species of *Stigonema*, a form of *S. informe* Kütz., and *S. hormoides* Born. and Flauh., the latter soon becoming more abundant and gaining the upper hand. The last arrival is *Schizothrix epiphytica*, n.sp. (Fritsch), and according to Dr Fritsch, who has kindly named the various species for me and analysed the succession, this species "has in many places almost completely enshrouded threads of the *Stigonema* with its red coiling filaments. Between the upright branches of *S. informe* and the *Schizothrix*, a struggle for supremacy is going on." The four species form an intimate association or what Fritsch (*New Phytologist*, 1906, p. 158) has called a "consortium." Similar successions were obtained from widely separated parts of the Drakensberg cliffs, e.g. at the Tugela Gorge, *Glæocapsa sanguinea* followed by the same two species of *Stigonema* and *Schizothrix epiphytica* together with *Calothrix parietina* (Naeg.) Thun. var. *africana* nov.

var. Fritsch and *Schizothrix Muelleri* Naeg. This first stage consisting of various lithophilous Cyanophyceae is exceedingly well developed in Natal. Very large areas of the cliffs are covered by it and are coloured black. In dry weather, it shrivels somewhat and peels off, restoring to some extent the original colour of the cliffs. The influence of climate on this earliest lithophilous stage is very marked. It demands warm, moist conditions and this it gets in the areas where it occurs. It has to withstand adverse conditions of drought and cold only during a comparatively short period and these adverse conditions are not so extreme on the cliffs of the Drakensberg as they are in the lower dry river-valleys. Though this stage is in general of an initial migratory nature, yet it must be considered the final stage for its own peculiar habitat, which is a very extensive one.

Turning now to the southwestern region of the Cape with its dry, hot summers we find lithophilous Cyanophyceae developed only in small patches where there is local moisture sufficient to overcome the general dry climate. I am again greatly indebted to Dr Fritsch, who has sent me the following information from samples which I collected on Table Mountain, Cape Town. The earliest colonist in this case is probably *Glæocapsa rupicola* Kütz. but the principal succeeding form is the interesting *Scytonema myochrous* (Dillw.) Ag. var. *chorographicum* W. and G. S. West. "This is the form," Dr Fritsch adds, "responsible for the so-called 'pedras negras' of Pungo andongo in Angola, where it apparently covers very considerable stretches of rock surface." Mingled with this *Scytonema* there is a good deal of *Schizothrix lardacea* Gom. which very probably formed the original base on which *Scytonema* settled down. Other species present are: *Stigonema tomentosum* Kütz. (in places the chief form growing on *Dichothrix orsiniana* Kütz. as a base), *Stigonema mamillosum* Lyngb., *Calothrix (parietina?)*, *Schizothrix* sp., *Nostoc microscopicum* Carm., *Mesotaenium violascens*, *Chroococcus turgidus*, *Navicula borealis* Ehrenb. and its variety *producta* Grun., *Zygnema ericetorum* var. *terrestre*. The occurrence of the last mentioned is interesting because it is found also on sandstone rocks in England. In one sample the main mass consisted of a new species of *Homoeothrix* which Dr Fritsch states he proposes to call *H. fusca*.

(2) *Lichen Associations*. In Natal, these are numerous but not individually extensive. They are found in drier situations than the last mentioned type and reach their best development outside the regions where summer mists prevail. The cliffs of Table Mountain, Cape Town, show a much more extensive lichen development than any of the cliffs in the eastern portion of South Africa, the climatic factors again being the determining ones. A dry, hot summer such as occurs in S. W. Cape is not favourable to the development of extensive associations of blue-green algae but does favour lichen development. Little, unfortunately, is known regarding the various species. The most abundant and characteristic in

the Cape Peninsula are, according to Marloth (15), *Parmelia conspersa*, *P. caperata*, *Physcia leucomelana*, *Pertusaria lactea*, *Umbilicaria rubiginosa*, *Xanthoria parietina*, *Trentepohlia occulta*. A species of *Pertusaria* I have often found replacing associations of Cyanophyceae.

(3) *Lithophilous Associations of Mosses and Hepatics*. This represents a distinctly new stage, which is prepared for by the previous stage or stages according to the law enunciated by Clements (vide supra). Some species, e.g. those belonging to the genera *Macromitrium*, *Brachythecium*, *Rhodobryum*, *Frullania*, *Orthotrichum*, *Fimbriaria*, etc., demand moist or fairly moist conditions, while others, e.g. species of *Grimmia*, *Dicranum*, *Campylopus*, *Andreaea*, *Brachymenium*, etc., can withstand extreme drought and strong insolation. In many places, there are wet rock flushes with ordinary green algae in great variety in addition to the mosses and hepatics. The determining factors therefore, both climatic and edaphic, are various, and strictly speaking we are dealing with separate successions. They could easily be divided on the lines indicated but to do so in this paper would lead us into too great details.

B. **Chomophyte Succession.** As denudation proceeds, shallow rock pans, ledges, holes and crannies appear and soil accumulates. The soil is partly derived directly from the rock itself, partly blown on or washed on to the rock surface from elsewhere. The amount and physical characters of the soil, the degree of moisture and of shade and shelter vary so that we get a variety of chomophytic types. Exposed Chomophytes, Sheltered Chomophytes, Shade Chomophytes, Hydrophilous Chomophytes, is a rough but convenient mode of classifying them. The species vary very greatly in different parts of South Africa, bearing a very obvious relationship to the surrounding formations. Lists were given for the Drakensberg in a former paper (3) and need not be repeated. They include mosses and hepatics in great variety, ferns, numerous bulbous plants, a few grasses, and in the more exposed situations, fleshy xerophytic species, *Crassulas*, *Mesembryanthemums*, etc. Many of the species are confined to this class and are never found elsewhere, but in addition there are numerous invaders from subsequent more stable types. Some of the invaders, however, never get beyond the seedling stage. All the above are migratory types. Cliffs and bare rock-surfaces give rise, by further denudation and disintegration to shingle slopes, talus or scree, and in the case of mountain tops to a special type of mountain-top detritus. The vegetation is at first chomophytic and the species are the same as occur on the cliffs. As stabilization proceeds, other species gain dominance. The climatic factors determine the ultimate stages.

FELLFIELD

The description given by Warming (30) of fellfield is as follows. "The soil is never completely covered by plants. One individual stands here and another there; between them we see bare, pebbly, stony, sandy or clayey soil, which is devoid of humus and determines the prevailing colour of the landscape." It is a description which would apply to great stretches of plant formation in South Africa, including much of the Karroo. However, even if Karroo does approximate in parts to fellfield, there is no reason why we should not retain such well-known terms as Karroo and Karroid to apply to that great region of the interior of South Africa. Outside the Karroo region, we get at higher altitudes on the Drakensberg and other mountains of the eastern side, as well as on the mountains of the southwestern and western sides, areas of typical fellfield. The first species are lithophytes and chomophytes (particularly lichens and mosses) such as have just been described. Other species growing isolated include xerophytic grasses, succulents especially Crassulaceae and Ficoideae (*Mesembryanthemum*), bulbous plants and orchids in considerable variety and sclerophyllous dwarf species of *Cliffortia*, *Erica*, *Phyllica*, *Muraltia*, *Coleonema* and various Compositae (*Euryops*, *Helichrysum*, etc.). The composition naturally varies in different parts of the country and like the chomophytic species is related to that of the surrounding formations. Probably we should include in fellfield, Marloth's "Karroide felsenheide" which is a succulent type corresponding closely with Karroo.

SCLEROPHYLLOUS FORMATIONS

The determining factors here are climatic. Sclerophyllous vegetation is characteristic of the southwestern region of the Cape, where the rainfall is mostly in winter and the summers are comparatively dry. The total amount, however, is not small, though it varies very much for different stations, exposure, etc., having a great effect. The total amount varies from about 300 to 1000 mm. (12 to 40 ins.), but Table Mountain, Cape Town, gets much more, 1592 mm. (64 ins.). Of the total rainfall, usually not more than 10 per cent. falls during the three summer months. The composition of the sclerophyllous formation of the Cape has been dealt with by numerous writers, the latest account being that of Marloth, beautifully illustrated. Details of the succession have still to be worked out. In the Cape Peninsula, the lichen associations above referred to form the earliest stage, followed by lithophilous mosses. An interesting chomophytic vegetation succeeds, including a great admixture of species. These vary with the degree of moisture available from extreme hygrophilous associations (which however are the most migratory of all) to very xerophytic types. The next stage in succession is represented in places by fellfield but generally by the Heath formation

(Marloth's "Hugelheide"). This invades the granite where the soil may be very shallow or very deep but always for several months of the year, is very dry. For full lists of species Marloth's work (**15**) should be consulted. The species *Blaeria ericoides* (Ericaceae) which recalls in some respects the *Calluna* of Europe is often dominant but there is always present a variety of other dwarf shrubs, e.g. *Cliffortia ruscifolia*, *Passerina filiformis*, *Sarcocolla squamosa*, *Rhus rosmarinifolia*, *Elytropappus rhinocerotis*, *Brunia nodiflora*, *Penaea mucronata*, *Leucadendron adscendens*, *Euryops abrotanifolius* and species of *Protea*, *Erica*, *Phylica*, *Polygala*, *Muraltia*, *Aspalathus*, etc., etc.; half-shrubby or herbaceous species such as *Leonotis leonurus*, *Peucedanum galbanum*, *Cyphia bulbosa*, *C. volubilis*, *Othonna tuberosa*, *C. amplexifolia*, *Salvia africana*, *Solanum sodomaenum*, *Hydrocotyle solandra*, species of *Selago*, *Scabiosa*, *Berkheya*, *Gerbera*, *Senecio*, *Helichrysum*, etc.; Restionaceae, e.g. *Restio cuspidatus*, *Elegia juncea*, *Thamnochortus cernuus*; Cyperaceae, e.g. *Tetraria cuspidata*, *Ficinia scariosa*; grasses, e.g. *Andropogon nardus*, *Danthonia macrantha*, *Cynodon dactylon*, *Stenotaphrum glabrum*, and species of *Andropogon*, *Ehrharta* and *Aristida*; ferns, e.g. *Mohria caffrorum*, *Cheilanthes hirta*, *Ch. capensis*, *Pellaea auriculata*; and a large variety of Monocotyledons, mostly bulbous, belonging to the families Orchidaceae, Haemodraceae, Iridaceae, Amaryllidaceae and Liliaceae—*Bobartia spathacea* is one of the commonest.

This Heath formation is closed and stable, and represents the climax type for its habitat. Migratory types however occur within it where springs or "flushes" emerge. On the slopes of Table Mountain underneath the sandstone and above the granite, we get a line of such flushes. In collaboration with Dr E. P. Phillips, I hope to make a further detailed study of these and investigate more fully, at the same time, the succession in the Heath formation. So far as our preliminary investigations went there are wet flushes with *Juncus lomatophyllus* dominant, drier flushes with the grass *Stenotaphrum glabrum* dominant, and dry or intermittent flushes with the moss *Archidium ecklonianum* dominant. The last mentioned may also represent an early stage in the Heath succession. Such flushes are conspicuous but not large. They extend for a short distance down the hillside below the point where the spring emerges. They may die out or continue as a rivulet or stream.

Along the stream-banks the type is also migratory but very characteristic, the species depending on the presence of telluric water. *Berzelia lanuginosa*, *Psoralea aphylla*, *Myrica aethiopica*, *Euryops* sp. and *Athanasia* sp. were noticed below the wet *Juncus* flush referred to above, but the stream-bank type here includes many other species, e.g. *Erica curviflora*, *Osmitopsis asteriscoides*, *Psoralea pinnata*, *P. aphylla*, *Dovea mucronata*, together with a host of smaller herbaceous forms. Moist spots on the hillside can be recognised by the dominance of such species. In fact, in a type like the

Heath formation, which includes so many shrubby species, various gradations in their water requirements might easily be recognised and the species grouped accordingly. A comparative experimental investigation into their relative transpiration rates, similar to one which I have in hand for certain Natal formations, would yield valuable information. Heath is a sclerophyllous formation in which the heaths (*Blaeria ericoides*, etc.) or heath-like forms assume dominance, and on the whole it is best perhaps to restrict the term to this type, though this hardly covers the whole of the type to which Marloth applies the term "Heide."

The **Macchia** (or **Mâquis**) is another sclerophyllous formation, much more extensive and including a variety of associations. The term Fynbosch is also applied to it locally—a term used to designate any sort of small woodland growth which does not include timber trees. Typical species belonging to Macchia include the following: *Olea verrucosa*, *Gymnosporia* (*Celastrus*) *laurina*, *Rhus glauca*, *Rhus* spp., *Myrsine africana*, *Leucadendron argenteum*, *Leucospermum conocarpum*, *Mimetes cucullata*, *Protea mellifera*, *Protea neriifolia*, *P. grandiflora* etc.; *Colpoön compressum*, *Passerina filiformis*, *Metalasia muricata*, *Cliffortia* spp., *Phylica* spp.; with Restionaceae and hundreds of other associated plants. The type however varies in different parts. Marloth's descriptions for the Macchia of Paarlberg, Tulbagh, Olifant's River and the coast region should be consulted. There are many places in which the coast Macchia shows a connection with the Karroo by the inclusion of succulents such as *Cotyledon fascicularis*, *C. cacalioides*, *Aloe* spp., succulent Pelargoniums, *Caralluma incarnata*, etc. The Eastern Macchia also shows a connection with the Eastern Bush by the inclusion of trees such as *Kiggelaria africana*, *Olinia cymosa*, *Podocarpus*, etc. At the same time, it is the climax type for its own climatic habitat.

Marloth gives details of the development of Macchia. A bare space, free from all the original vegetation, in the second year showed typical Heath formation which was gradually followed by the larger Macchia species.

The Rhenosterveld, in which the Rhenosterbosch (*Elytropappus rhinocerotis*) is dominant together with grasses, e.g. *Cynodon dactylon*, *Tristachya leucothrix* (a characteristic mountain species of the Drakensberg), *Pentaschistis airoides*, *Lasiochloa ciliaris*, *Vulpia bromoides* and a great variety of associated plants, covers large areas in the districts of Stellenbosch, Paarl, Wellington, Malmesbury, Piquetberg, Tulbagh, Ceres and Caledon, but is, as Marloth points out, not a natural but a "Kunstformation" following as a result of man's cultivation and interference (cf. the "Changed Veld" of the eastern side of South Africa).

On the flat top of Table Mountain, where the rainfall is much greater (over 60 inches), there is a more mixed type, which Marloth designates "Bergheide." This mountain Heath, however, can hardly be classed as a single formation. There are all possible gradations of water-content. The

bare exposed rock-surfaces are often covered with mats of *Campylopus atroluteus* and other xerophilous mosses. In the innumerable moist krantzies, on the other hand, the rock surfaces support an extremely hygrophilous mixture of associations. *Sphagnum* (*S. capense*) hangs in festoons and masses from the edges of dripping waterfalls. There is an endless display of leafy and thallose hepatics and hygrophilous mosses, such as *Wardia hygrometrica*, *Schistochila alata*, *Plagiochila asplenoides*, *Lepidozia laevifolia*, *Lepicolea ochroleuca*, *Jamesoniella colorata*, *Frullania diptera*, *Metzgeria furcata*, *M. nudifrons*, *Neckera pinnata*, *Aneura pinnatifida*, *Radula complanata*, *Symphogyna podophylla*, *Leucoloma zeyheri*, *Philonotis afrofontana*, *Marchantia polymorpha*, *Anthoceros punctatus*, *Fissidens fasciculatus*. Mixed with these are filmy ferns (*Trichomanes pixidiferum*). As soil gathers, there appear other ferns and flowering plants, e.g. *Acrostichum conforme*, *Todea barbara*, *Gleichenia polypodioides*, *Hymenophyllum tunbridgense*, *Cliffortia odorata*. The most beautiful of the Cape orchids (*Disa uniflora*, *D. grandiflora*) are found here. In more exposed swamps, over the flat mountain-top, various species of Restionaceae (*Restio compressus*, *Dovea mucronata*, *Elegia acuminata*, *Thamnochortus dichotomus*, etc.) are dominant with numerous other plants associated such as *Berzelia lanuginosa*, *Watsonia meriana*, *Disa graminifolia*, *Erica curviflora*, *Psoralea aphylla*, etc.

On the drier parts, the succession is entirely different, resulting in fellfield, heath or macchia. There are numerous species of *Erica* (*E. lutea*, *E. coccinea*, *E. physodes*, *E. gilva*, *E. hirtiflora*, *E. hispidula*, *E. calycina*, *E. petiveri*, *E. tenuifolia*), *Brachysiphon fucatus*, *Gnidia oppositifolia*, *G. pubescens*, *Selago serrata*, *Staavia glutinosa*, *Cliffortia ruscifolia*, *Protea cynaroides*, *P. speciosa*, *Leucadendron grandiflorum*, *L. decorum*, *Mimetes cucullata*, *Priestleya villosa*, *Aspalathus anthyllioides*, *Helichrysum vestitum*, and innumerable others. Much further attention should be given to the analysis of this most interesting and complex type. The succession will be found to be partly towards the hydrophilous and mesophytic, a migratory type, depending entirely on the topography which influences for a time the climate, but mostly towards the sclerophyllous ending in Heath or Macchia as the climax type. Macchia or Fynbosch is the chief plant formation in the southwestern region, but not the only one. The coast succession there will be referred to later and the Bush, of which there is very little, will also be considered along with that of the eastern side. Macchia however is not confined to the southwestern region. It extends eastward along the mountain ranges and in the Drakensberg range bordering Natal at high altitudes, 7000–8000 feet and over, the climatic factors continue to produce a type of Macchia with *Cliffortia linearifolia*, *Myrsine africana*, *Metasias muricata*, *Passerina filiformis*, *Erica* spp., and a variety of others. A fuller list of species I have given in a former paper (3). As we pass from the western side where the rainfall is mostly in winter to the eastern side where rain falls chiefly in

summer, the Macchia becomes more and more of a mountain type till in the Drakensberg, it is not found below an altitude of 7000 feet.

ALPINE OR SUB-ALPINE TYPES

The vegetation of such flat-topped mountains as Table Mountain, Cape Town, the altitude of which is less than 4000 feet, cannot be classified as alpine. It is true the climatic factors differ from those of the lower slopes, the amount of rainfall being increased, but this only tends to produce a more mixed type. On the tops of the higher mountains however, we get a true alpine type, the altitude of which increases as we proceed eastward and northward towards central Africa. The growth forms are of the usual alpine character, spreading or mat-forming dwarf shrublets, cushion-forms, rosette-forms, succulent forms, etc., many of them with large, thick, woody roots. For a list of species occurring on the higher peaks of southwestern Cape Colony, Marloth (15) may be consulted. I have also given a brief description of the "Formation of Mountain-top Detritus" as occurring on the Drakensberg at an altitude of 10,000 feet, in a former paper (3). Marloth calls the formation "Sub-alpine Felsenheide" and, in part at least, it corresponds to Warming's "Fellfield" (30).

EASTERN SCRUB

This is similar and not very far removed from Macchia but it is more mesophytic. It occurs in the region of summer rains and is often transitional to Forest. It does, however, in places, possess a certain degree of stability of its own. The Oudehout Scrub of the Drakensberg with *Leucosidea sericea* dominant, *Buddleia salviaefolia* frequently sub-dominant, and a number of other species such as *Myrsine africana*, *Heteromorpha arborescens*, *Cussonia spicata*, *Rhus* spp., *Royena* spp., etc. mixed—for full description see Bews (3)—is one of the best developed examples. It follows on the Macchia or Fynbosch of the higher altitudes and around its margins we often get sclerophyllous species such as *Cliffortia linearifolia*. Oudehout Scrub is much denser than Macchia, the branches of the trees interlacing, so that it is often quite impenetrable. At lower altitudes, *Rhus* spp., etc. may form similar scrub without Oudehout (*Leucosidea*). Oudehout Scrub in addition to invading Macchia, often colonises new ground. The *Leucosidea* itself is frequently the first species found in rocky stream channels at high altitudes on the Drakensberg. The succulent and thorny scrub with *Euphorbias*, *Aloes*, etc., of the dry river valleys at lower altitudes is of quite a different character and is best considered later.

FOREST

Bush is the term applied to High Forest in South Africa, and it is confined for the most part to the region of summer rainfall. The rainfall over the whole eastern side varies from about 25 to 45 ins. (600 to 1000 mm.) of which about 70 per cent. falls in summer. The total annual rainfall is thus not appreciably greater than in the region of sclerophyllous types, but the prevalence of summer over winter rains has a pronounced effect on the vegetation. Even within this region, however, a forest climate occurs only in certain places where the rainfall and deposition in the form of mist, protection from dry hot winds and the gradient to provide for cold-air drainage are suitable. The Bush therefore occurs only on the slopes with a southeastern aspect facing the Indian Ocean. The rest has Grassland as its climax type. The Bush may conveniently be classified into Mountain, Midland and Coast-belt types, the term Midland being taken as applying only to the region where Bush occurs and not to South Africa as a whole. Bush is quite stable within the limits of its (climatic) habitat, and as Clements points out, "forest is the last stage for all mesophytic habitats." As a result of man's interference, however, Grassland may invade the true Forest habitat, but unless prevented by the constantly recurring grass-fires Bush will re-establish itself. As forest becomes established certain progressive changes take place in the habitat. The first species are light-demanding, but they grow sufficiently close together to provide shelter for the seedlings of the more ombrophilous forest species. When these grow up they produce denser shade and the first stage disappears or retreats to the margin. Light however is only one of the factors to be considered. Temperature, particularly winter low temperature, is of importance as helping to differentiate between Coast, Midland and Mountain types. Moisture is increased as the Bush develops and the soil characters are altered, the amount of humus increasing. The sum-total of the changes results in a more mesophytic habitat. Biological factors are also of importance in certain cases. Insects regularly destroy the seeds of certain species of trees, and in forestry practice it is difficult to obtain seedlings though plenty of seed is formed.

Our knowledge of the exact requirements of the separate species is not yet very exact, though Sim's "Forests and Forest Flora" (24) contains a large amount of information, and I am further indebted to the author for much direct assistance. Mr J. S. Henkel, now Conservator of Forests for Natal, has also kindly interested himself in the problem and has supplied me with information, as mentioned in the account which follows. At present, I can only give an outline sketch of the probable succession, which applies chiefly to Natal:

FIRST STAGE. (a) On the Drakensberg. *Leucosidea sericea*, *Greyia sutherlandi*, *Myrsine africana*, *Aloe natalensis*, *Heteromorpha arborescens*,

Arundinaria tessellata and other species included in my previous descriptions of Oudehout Scrub (3). (b) In the Midlands. Some of the above, such as *Greyia*, *Aloe* and *Heteromorpha* together with *Commiphora harveyi*, *C. caryae-folia*, *Panax gerrardi*, *Halleria lucida*, etc. (c) On the Coast. *Cussonia umbellifera*, *Commiphora* (both species), *Schmidelia monophylla* and others. All the species in the first stage are light-demanders and none of them continue after the bush closes over.

SECOND STAGE. Incursion of the more permanently leafy forms, giving a closer canopy and denser shade, and increasing the amount of moisture: *Rhus* spp., *Royena* spp., *Euclea* spp., *Celastrus* spp., and in the Midlands *Ehretia hottentotica*.

THIRD STAGE. This is, for the most part, the final stage. Under the conditions produced in the second stage, the tall forest trees grow up and commonly the yellowwood species, *Podocarpus thunbergii* and *P. elongata*, finally become dominant in the Mountain and Midland Bush, while *Rhus longifolia* and *Albizzia fastigiata* are frequently dominant in the Coast Bush. The general ecological character of the Bush, as represented by this stage, is not extremely mesophytic. The species are mostly somewhat xerophilous in character, very hard-wooded and slow-growing, with hard leaves. Epiphytes are not abundant, though several interesting species occur. There is, however, a large number of lianes of the pliant, ropy or thick woody types and this increases the mesophytic nature of the Bush as a whole.

In different parts of the country, there is considerable variation in the composition. Full lists for the more important Natal forests were given in former papers (1, 2, 3) and for Cape Colony Sim (24) records the distribution of the main species. There is always a large admixture of species in every Bush and instead of yellowwood, the sneezewood (*Ptaeroxylon utile*) or the black stinkwood (*Ocotea bullata*) or the black ironwood (*Olea laurifolia*) or occasionally other species may become dominant. Further research will be necessary to explain these differences. An investigation into the transpiration rates and water requirements of the different species has been begun and it is hoped this will throw some light on the problem. Careful mapping and counting of the species on selected areas or strips will also assist us. The following will serve as an illustration. The species *Podocarpus falcata* has become completely dominant in some of the forests of East Griqualand and the Polela district in Natal. In the Insikeni Forest, E. Griqualand, a true virgin area, two acres in extent was marked out in 1900 and the increase in growth of the trees has been measured in 1903, 1906, 1908, 1913. I am indebted to Mr Henkel for supplying me with the details. The percentage composition works out as 60 per cent. *Podocarpus falcata*, 14 per cent. *P. elongata*, 19 per cent. *Ptaeroxylon utile* and 7 per cent. others. The figures, however, for trees of different diameter allow us to draw other important conclusions. Having determined the annual rate of increase, from the diameter measurements one can

gauge fairly accurately the age of the separate trees. Such a table as the following, therefore, gives a certain amount of information regarding the past history of the Bush, though conclusions in this respect must be accepted with caution, for we have no means of telling what trees have died out altogether. The table gives more definite information regarding the present regeneration and the progressiveness or retrogressiveness of the separate species. The falcate yellowwood is completely dominant and shows the best regeneration. It is ousting the common yellowwood, of which there are few young trees. Sneezewood, however, is fairly progressive, but it has not reached the size of the falcate yellowwood.

Species	Total number of trees	Diameter of stem in inches																											
		2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	38	40	42	44	46	48	50	52	54	
Podocarpus falcata	140	41	18	12	10	4	8	4	2	6	5	4	2	3	4	1	1	2	3	2	2	2	1	—	1	1	1	—	
Podocarpus elongata	34	2	5	5	2	1	3	3	2	1	5	1	—	—	1	—	1	1	—	—	—	1	—	—	—	—	—	—	
Ptaeroxylon utile	48	17	3	4	4	3	3	2	1	2	—	3	3	—	2	—	—	1	—	—	—	—	—	—	—	—	—	—	
Olea laurifolia	4	1	—	—	—	1	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Toddalia lanceolata	4	1	1	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Celtis kraussiana	2	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Scolopia ecklonii	2	1	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Calodendron capense	2	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Nuxia floribunda	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Elaeodendron croceum	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	

The effect of differences in the soil conditions, though not so important as climate, must not be overlooked. The majority of the forests occur on a soil derived from sandstones, sandy shales and dolerite, and is of the loose, well-aerated, high-veld type. The Ngoya Forest, however, occurs on a soil derived from metamorphic rocks (quartzites, schists, gneisses) and intrusive granite and is peculiar also in its topography. It occupies a number of minor hills and valleys in the centre of a main range. *Milletia sutherlandi* (bastard umzimbeet) is completely dominant, while the yellowwood (*Podocarpus thunbergii*) is rare. The Egossa Forest in Pondoland is derived in part from similar rocks and is of a mixed type. In the Intsubani Forest also in E. Pondoland, Sim notes again the high proportion of *Milletia sutherlandi*. Sim also points out that *Rhus erosa* and *Rhus dregeana* are present only on dolerite, that the black stinkwood (*Ocotea bullata*) is totally absent from Kaffraria while it is abundant east and west of it and that the Proteaceae are absent from calcareous soils. Such soil influences on individual species are of more importance than on the bush as a whole.

The species *Xymalos monospora* (lemonwood) deserves special mention, for it may possibly represent a fourth stage in Bush succession. It is able to survive intense shade in the seedling stage and itself at maturity has such dense foliage as to kill out all other seedlings. It withstands fire, too, and is well fitted to assume dominance, which it has done in places. It is however, limited by its water requirements, being more mesophytic than the others. This in itself indicates its place in the succession. Mr Henkel suggested to me that it may be a newcomer, and possibly this is true. Mr Sim informs

me that it extends northwards through the mountainous parts of Portuguese East Africa. It is a monotypic South African genus and the only member of the Monimiaceae found here.

In dealing with the composition of the Bush, great care must be taken to distinguish the truly virgin forests from those that have been worked. A very false picture may be presented if the percentage composition be taken of the present forests as supplied in the forestry returns. Care should be taken to ascertain what species have been felled. The composition of the Knysna forests, as given by Marloth (15) does not give a true picture of the natural composition. He gives *Olea laurifolia* as most abundant but this is simply because *Olea* has been left alone while the yellowwood has been to a large extent cut down.

After bush-fires, the succession can be easily followed. *Rubus pinnatus* is a characteristic species, almost invariably one of the first to arrive. *Xymalos*, however, if present, often survives the fire. The first growth is of herbaceous and shrubby species followed by the seedlings of the forest trees. It must not be assumed, of course, that the succession after a fire is a true topographical succession. It will naturally depend largely on the species originally present. The following list gives some of the commoner species in the early stages of the succession after fire: *Rubus pinnatus*, *Chilanthus dyssophyllus*, *Berkheya* spp., *Athanasia acerosa*, *Buddleia salviaefolia*, *Asparagus* sp., *Pteris aquilina*, *Andropogon* spp., *Solanum* spp., *Physalis* (Cape Gooseberry), *Senecio juniperinus*, etc.

In Knysna, a marked succession has been noted by Henkel (14). The species *Virgilia capensis* (keurboom), the seeds of which become widely disseminated whenever a fire occurs in the forest or the soil of the veld has been disturbed, quickly forms thickets which gradually become replaced by high forest trees growing up in the shade thus produced. Numerous instances, Henkel states, of the undoubted reclamation and extension of High Forest brought about by keur, are to be met with. It is such observations as these that we look for, from those in a position to record them.

In the Cape Peninsula, Bush replaces Macchia, as already mentioned, on the slopes of Table Mountain which face the southeast winds, and in the western forests Macchia species are often marginal to Bush, again indicating the succession.

MIGRATORY TYPES OF BUSH

Various migratory types have been recognised and described. The Stream-bank Bush of higher altitudes, with *Widdringtonia cupressoides*, *Ilex capensis*, *Ficus capensis*, *Myrsine melanophleas*, *Rhus* spp., *Erica* spp., *Myrica aethiopica*, *Aberia tristis*, *Arundinaria tessellata* and dwarfed yellowwoods, is clearly of a migratory character (3). In the same way, the Bush which fills the smaller stream valleys at various altitudes with such species as

Rauwolfia natalensis, *Trema bracteolata*, *Combretum kraussii*, *C. salicifolium*, *Celtis kraussiana*, *Rhamnus prinoides*, *Ficus natalensis*, *F. capensis*, *Voacanga thouarsii*, *Halleria lucida*, etc., is also migratory (1, 2). Ecologically these migratory types differ from the other Bush in being more open and since more light penetrates, the undergrowth of smaller shrubs and herbs (including grasses sometimes) is more luxuriant. The habitat is obviously of an unstable type.

STREAM-BANK BUSH AND SCRUB OF THE DRY INTERIOR

In the arid Karroo region and the interior and west side of South Africa generally, migratory Stream-bank Bush assumes great importance as an ecological type. Tree growth is dependent in this case entirely on the presence of the stream and river water. A fairly close connection is shown with Tree Veld and Succulent and Thorny Scrub. I am able to give a detailed description of one of the best examples of this type, through the kindness of Mr Henkel, who explored the lower Orange River Islands between Upington and Keimos. He has handed over to me a copy of the report, which he made, dated November 1908. The Orange River is the only running water present in a great tract of country and in the part explored by Mr Henkel flows over a hard rock-bed with little fall. The river, in times past, on account of the more or less level nature of the country, has divided itself into a great number of streamlets spreading over an area, varying from one-half to six miles in width. The islands, which were originally merely slight elevations, have become more prominent in course of time by the deepening of the channels between them and they have been extended by the deposition of silt. The vegetation binding the silt is of so tenacious a nature that once an island is formed, it does not readily disappear. Changes in the water level are, however, reflected in the vegetation. Along some of the courses, water has now ceased to flow, except in exceptionally heavy floods and, in such cases, the trees are dead or dying. The intensely dry atmosphere prevents rapid decay of the dead trees and there is an accumulation of dead material such as Mr Henkel has never seen before. "The effect," he says, "is extremely depressing." This illustrates very well the migratory nature of the formation. As soon as the river water is withdrawn, the vegetation dies, and it is particularly interesting to find that even when dead it holds the ground for a very long time.

Where the water is still available, a green fringing belt marks the perimeter of the islands and extends along the main banks of the river. The width of the fringe averages about 15 metres but exceptions occur, where on account of the presence of subterranean water, the width may extend to the whole island, particularly in those of more recent formation. The following were the species of trees or tall shrubs composing this Stream-bank Bush: *Salix capensis*, *Combretum erythrophyllum*, *Rhus lancea*, *R. viminalis*, *Zizyphus*

mucronata, *Royena pallens*, *Acacia horrida*, *Olea verrucosa* (in rocky places near rapids), *Tamarix articulata* (in "brak" places) and *Acacia giraffae* (in drier parts where however the soil is good, rarely near banks of the stream-lets). The species are named more or less in the order of their succession. They are all characterized by extraordinary powers of coppicing and in the case of *Royena*, of developing abundant stool shoots and root suckers. *Salix capensis* is most abundant in this place, and usually grows nearest the water. The roots are the most powerful factor in holding the loose silt and causing further deposition. The floor of this Bush is, as a rule, destitute of any growth. Regeneration from seedlings is extremely rare, except in the case of the willow, the seed of which grows freely in the wet mud on the banks. In many cases, the wide branches of the various species have been lopped for fodder for goats. Whenever this happens, fresh coppice shoots are sent out and in a few years, the shrubs are full crowned again.

Numerous references to the same type are made by almost every writer who has described the vegetation of such regions as the Karroo, S. W. Africa and the interior. In the dry river beds of the typical Karroo (the Gouph) in places *Tamarix articulata* alone is found; in other places, *Acacia horrida* (sometimes with *Viscum rotundifolium*), *Salix capensis*, *Rhus viminalis*, *Salsola aphylla*, *Atriplex halimus*, *A. nummularia*, *Lycium* spp., *Gomphocarpus fruticosus*, *Melanthus commosus* and the grasses *Aristida namaquensis*, *A. vestita*; in the western portion of the Great Karroo, *Rhus viminalis*, *Royena pubescens*, *Zizyphus mucronata*, *Phragmites communis* and *Scirpus* spp. In S. W. Africa, according to Wagner (29), the type consists of *Acacia albida*, *A. horrida*, *A. giraffae*, *Euclea pseudebenus*, *Tamarix austroafricana*, *Combretum primigenium*, *Zizyphus mucronatus*. Pearson (18, 19) in his account of his journey from the Cape to S. W. Africa, makes frequent reference to the type, mentioning as belonging to it *Tamarix* (sometimes with *Viscum*), *Acacia horrida*, *Rhus viminalis*, *Salix capensis*, *Euclea pseudebenus*, *Sisymbrium sparteum*, *Zizyphus mucronata*, *Hoodia* sp., *Rhigozum trichotomum*, *Cataphractes alexandri*, *Parkinsonia africana*, etc.

GRASSLAND

In some respects it might be considered more natural to deal with this before the Bush, since Grassland is less mesophytic and in some cases is an earlier stage in the succession to Bush. In South Africa, there is no evidence to show that this is the case. Our climate is only locally a forest climate and Grassland covers a far larger area in which it is the final stage. Indeed, as already pointed out, in many cases grassland has even invaded the true forest habitat. Forest, so far as we can trace its development, follows directly on Scrub and that on chomophytic vegetation. Grassland is not an intermediate stage. Forest and Grassland are therefore here put on an equal level, each being the final stage for its own habitat. There are, however,

intermediate types of Tree Veld to be considered later. Grass Veld may originate in the following different ways:

(a) Through the invasion by veld grasses of open or semi-open formations, formed on the soil produced as the result of the disintegration of the underlying rock. Lithophytes and chomophytes precede and sometimes Fynbosch or Heath formation forms an intermediate stage. In the typical Heath formation of the Cape, grasses are by no means absent, but they grow in tufts intermingled with other plants. In some cases, however, the grasses themselves are among the earliest arrivals. For a considerable time, the formation remains unstable. There are a large admixture of associated Veld plants; in fact it may be taken as a general rule that the more numerous these are, the further removed from complete stabilization is the Grassland formation. On the Drakensberg and other mountains, a well marked stage is represented by Tussock Veld, the alpine species of grasses (e.g. *Harpechloa capensis*, *Microchloa caffra*, *Koeleria cristata*, *Eragrostis* spp., *Anthoxanthum ecklonii*, *Tristachya leucothrix* and a variety of others) growing in more or less isolated tufts and tussocks. There is great variety of associated flowering plants present, and the type is unstable. So also on the hillsides at lower altitudes, tall species of *Andropogon* with numerous associated plants form another unstable or migratory type. The final stage is represented by large stretches of veld, where *Anthistiria imberbis* is completely dominant and the associated plants are few—a comparatively stable condition.

(b) Through soil being blown on to bare rock surfaces. The stages in the succession are essentially similar to the above.

(c) Through the invasion of river beds and the colonization of alluvial soils. The soil here is of a compact, clayey nature, badly aerated but richer in chemical salts than the loose well-aerated soil of High Veld. The pioneer grasses are species of *Aristida*, *Pennisetum*, *Setaria*, *Andropogon* and Vlei species, including numerous Cyperaceae, all representing migratory types, but the final stage is again *Anthistiria imberbis* (the distinct variety which is dominant in Low Veld).

(d) Through the silting up or drying up or draining out of Vleis and the displacement of Vlei grasses and Cyperaceae by Veld. The tall *Andropogon* species, especially tambootie grass (*A. marginatus*) and other grasses here give us an intermediate type.

(e) Occasionally by replacing Bush as indicated above. Once more the unstable *Andropogon* associations precede.

The conditions of geological stability with resulting stable plant formation only last for a time. Denudation continues and the level parts are intersected by ravines or dongas. The rapidity with which such dongas are formed and increase in size never fails to impress those making acquaintance with South African conditions for the first time. On the resulting slopes where the ground is freshly laid bare, a new succession is initiated. We

get invasion of bare rock surfaces by lithophytes and chomophytes again, and then grasses reappear, *Andropogon* and *Aristida* spp., etc., with numerous associated plants holding the ground for a time and being gradually ousted by *Anthistiria* as stabilization proceeds. Ravines, however, as pointed out above, are often taken possession of by the migratory types of Bush and if the climate, as a result of the rearranged topography, is suitable, the final stage may be Bush. There may thus be an interchange between Bush and Grassland as denudation proceeds.

There remains one notable succession in Grassland which is of a secondary nature due to man's interference and the continual burning of the grass, namely the replacement of *Anthistiria imberbis* by *Aristida junciformis*. This I have designated "Changed Veld" for want of a better term (2). Such changed veld is very extensive in parts of Natal. Other species, such as *Sporobolus indicus*, *Eragrostis curvula*, *Cynodon dactylon* are sometimes dominant in changed veld.

With increasing aridity, the typical *Anthistiria* Veld of the eastern side gives way to a semi-open type, where *Aristida brevifolius* (toa grass) grows in isolated tufts. Still more xerophytic conditions cause the almost complete disappearance of grasses and the substitution of the succulent and sclerophyllous dwarf shrubs which make up the Karroo formation.

COMPOSITAE VELD

North of the Karroo, we get a region differing from it floristically in having fewer succulents and a high proportion of Compositae. This formed one of Bolus' main floral regions—the Upper Region. Marloth calls it "Karroide Hochland." The amount of rainfall increases from west to east as does also the prevalence of summer rains over winter. Ecologically it may be considered as transitional between Karroo and Grassland. Among the Compositae in this region, the largest genera are *Senecio* (86 species), *Helichrysum* (71 species), *Othonna* (23 species), *Berkheya* (21 species), *Felicia* (17 species) [Bolus (5)]. There is, however, a fair proportion of succulents belonging to the genera *Crassula* (40 species) and *Mesembryanthemum* (23 species), and there are also Scrophulariaceae, Ficoideae, Asclepiadaceae, etc. Among the commonest species are *Pentzia globosa*, *Chrysocoma tenuifolia*, *Tripteris spinescens*, *Pteronia glomerata*, *Gazania longifolia*, *G. pinnata*, *Arctotis stoechadifolia*, *Hermannia spinosa*, *H. linearifolia*, *Aptosimum depressum*, *Mesembryanthemum nobile*, *Aloe aristata*, *Stapelia* spp., *Hoodia gordonii*, *Lycium arenicolum*, *Buphane disticha*, with a fair proportion of grasses, *Anthistiria imberbis*, *Aristida obtusa*, *Schismus fasciculatus*, etc.

VLEIS (MIGRATORY)

This is a distinctly migratory type, again comparable with the "Flushes" already referred to, in fact most of our vleis are simply flushes caused by

streams spreading themselves out over flat ground or by springs. Sometimes, however, vleis are formed in hollow rock pans or volcanic pipes and occasionally on the coast-belt as the result of silting-up. The succession is an interesting one, which I have given in a former paper (2) by classifying vleis according to wetness and degree of stagnation in the water. The first stage is represented by purely aquatic plants, various green algae together with *Nymphaea stellata*, *N. capensis*, *Utricularia* spp., *Potamogeton* spp., *Aponogeton natalense*, *Lemna*, *Callitriche*, etc. Then follows *Typha capensis* which grows in stagnant water. Next are found species of *Cyperus* (*C. latifolius*, *C. fastigiatus*, etc.) with typical vlei grasses (*Phragmites communis*, *Erianthus capensis*, *Leersia hexandra*, *Setaria aurea*, etc.), *Andropogon* spp., are mostly transitional to veld. Associated vlei plants such as *Gunnera perpensa*, *Richardia africana*, various orchids, etc., are very abundant. The above applies chiefly to Natal vleis. Marloth (15) gives a well-illustrated account of the Cape vleis. The stages are essentially similar to the above, but the species differ. *Nymphaea stellata*, *Limnanthemum thunbergianum*, *Potamogeton pusillum*, *Aponogeton distachyon*, *Oxalis natans*, *Scirpus ludwigii*, etc., form the earliest aquatic stage ("Limnäenformationen"), while *Typha*, *Phragmites*, *Prionum palmita* (Palmiet), *Richardia* (*Dantedeschia*) *aethiopica*, *Salix capensis*, *Cyperus* spp., *Cliffortia odorata*, etc., form succeeding stages of swamp—cf. also the flushes and migratory types in the Heath formation.

TREE VELD (GRASSLAND WITH SCATTERED TREES)

This is one of the most extensive of all the vegetation types in South Africa and it may be divided into several formations or sub-formations. The trees grow isolated or semi-isolated in the Veld, giving a park-like appearance. It is the Baum-Steppe of the German ecologists which we may translate as Tree Veld as far as South Africa is concerned. The following types of it occur.

1. **Acacia Veld or Thorn Veld of the Eastern side.** The soil in this case is a dry, hard, compact and badly aerated clay which is usually rich in chemical salts. The climate is dry and hot. Typical Thorn Veld occurs in the river valleys of Natal and the eastern side of South Africa generally. Thorny species of *Acacia* are dominant but other species also occur, e.g. *Celastrus buxifolius*, *Zizyphus mucronata*, *Sclerocarya caffra*, *Hippobromus alata*, *Ehretia hottentotica*, *Cussonia spicata*, *Euclea undulata*, *Chilianthus dyssophyllus*, *Nuxia floribunda*, *Rhus* spp., etc. The trees of the Thorn Veld in reaction to the adverse climatic factors, commonly assume the umbrella growth-form, with wide-spreading crowns and laterally extended root systems.

2. **Protea Veld.** The species of *Protea* composing this type prefer a loose well-aerated sandy soil, derived from sandstone or dolerite, poor in salts, especially lime. They occur at higher altitudes as on the Drakensberg

(3). *Protea roupelliae* is the most abundant there, but there are half a dozen other species. For Southern Rhodesia, Miss Gibbs (13) mentions that *P. abyssinica*, which also is common on the Drakensberg, is dominant on the "Sand Veld" near Fort Usher. Soil conditions are undoubtedly of importance in determining this type.

3. **Bush Veld.** This is the term applied to Tree Veld in the Northern and Northeastern Transvaal. It may be described as a Combretaceous-Leguminous type, the characteristic species being *Terminalia sericea*, *Combretum apiculatum*, *Burkea africana*, *Peltophorum africanum*, *Ficus cordata*, *F. capensis* and *Faurea saligna*, with occasional Acacias, *Cussonia spicata*, etc. Tree ferns (*Cyathea dregei*) grow to a large size near water. The presence of Aloes and Euphorbias, with species of *Mesembryanthemum*, *Kalanchoe*, *Stapelia*, *Anacampseros*, etc., on dry rocky hillsides indicates a connection between Bush Veld and succulent types to be considered later—Succulent Scrub and Karroo.

4. North of the Witwatersrand, according to Marloth (15), *Dombeya densiflora*, *Croton gratissimum*, *Chrysophyllum magalismontanum*, *Barbacenia retinervis*, *Cissus* spp. and *Protea hirta* form a distinct type, showing connection with Tree Veld of the interior.

5. In the Tree Veld of Rhodesia, south of the Zambesi, Miss Gibbs (13) states that *Combretum terminalia*, *Bauhinia* and *Sterculia* spp. with *Azelia cuanzensis*, *Peltophorum africanum*, *Copaifera coleosperma* and *Adansonia digitata* (baobab) are the commonest. She also notes the presence of *Oncoba spinosa*, *Ximenia caffra*, *Diplorrhynchus mossambicensis*, *Royena pallens*, *Olex dissitiflora*, *Bolusanthus speciosus*, and *Vitex flavescens*. "Tree Veld appears to be the vegetative type for the whole country."

6. The Western Transvaal, Bechuanaland and the central plateau of S. W. Africa are all either Veld or Tree Veld, with bare waste tracts becoming increasingly arid towards the west. The Bush Veld gives way to Thorn Veld and that in turn to semi-desert in places. According to Sim (24) a large proportion of the former timber vegetation of this region consisted of the large Camelthorn (*Acacia giraffae*), *Acacia detinens* and *Olea verrucosa* with *Acacia horrida* near streams and springs but within a hundred miles of Kimberley those have now mostly disappeared, being used up for firewood.

In S. W. Africa, the toa grass (*Aristida brevifolia*) covers large areas of Great Namaqualand with the trees *Acacia giraffae*, *A. detinens*, *Aloe dichotoma*, *Boscia foetida*, *Rhigozum trichotomum*. Northward in Damaraland, *Acacia albida*, *Acacia* spp., *Albizzia anthelmintheca*, *Boscia pechuelii*, *Dichrostachys nutans* and *Euphorbia* spp. Schinz (23) calls the eastern edge of Namib desert, which will be referred to later, "Euphorbia Steppe." The Tree Veld of this region, like that of the Transvaal, becomes more mesophytic as we proceed eastward. Still further north, according to Wagner (29) "east, and south-east of the Otavi Range, the plains have the character of gently

undulating expanses of tree steppe, the aspect of which is rendered distinctly tropical by the presence of tall, graceful palms (*Hyphaene ventricosa*). To the north and north-east of the range, they are, for the most part, covered with open forest, interspersed in the vicinity of Omuramba Ovambo with glades of delightful park land." The stream-bank types of S. W. Africa have already been dealt with.

7. Still further north in Angola, Pearson (**18, 19**) describes types in which *Copaifera mopane* is the dominant tree. The undergrowth, he says, is very rich in grasses, also including Pedalineae, Oldenlandieae, *Monsonia*, Acanthaceae, Capparidaceae and Leguminosae. Evidently it is a mesophytic type, not far removed from true forest, into which it passes. Pearson also notes the presence of Acacia Veld and Baobab Veld in this region. So far as can be judged it appears similar to the Rhodesian and eastern regions of the same latitude. The above types are all ecologically distinct but the arrangement given is a purely geographical one. Tree Veld can be subdivided ecologically into at least the following types: (1) *Euphorbia* Veld, (2) Acacia Veld, (3) *Protea* Veld, (4) *Terminalia* Veld (Leguminous Combretaceous type or Bush Veld), (5) Baobab Veld, (6) *Copaifera* Veld. These are named roughly in the order of increasing mesophytism, but doubtless there are others and much further attention should be given to determining the requirements of the various species. The more xerophytic types mentioned connect with Succulent and Thorny Scrub.

Tree Veld covers an enormous area in South Africa extending as it does from Portuguese East Africa right across Rhodesia, the Northern Transvaal, Bechuanaland and S. W. Africa to the Namib. It extends northwards along the coast to the Congo and much of Central and Eastern Africa is of the same type. It fills all the dry river valleys of the south-east side except in places where Succulent Scrub occurs. Its ecological history and significance is therefore of great importance. It is obviously intermediate between Grass Veld of the ordinary type without trees and Close-bush or Forest. Two views are possible regarding its origin. First it may be regarded as the remnants of a previous closer type of bush, which has become retrogressive either through a change in climate or owing to the influence of grass-fires. This view is commonly supported, but it involves certain difficulties. Grass-fires presuppose the presence of grass, and therefore could hardly have been a factor which would lead to a change from Bush to Tree Veld, since grass was not present in the former. Nor is there any real evidence of any pronounced change of climate, sufficient at any rate to explain the very great effect on the vegetation. The species in the Tree Veld are all light-demanders and could not have existed in dense Bush. It would be necessary to suppose, therefore, that the previous Bush species have entirely disappeared from those great areas and have been replaced by the other species at present found there. The present type must have existed for a very long time, for the

various types of mammals (springbok, etc.) are not adapted to forest conditions and they are extremely numerous in point of species.

The other view is to regard the Tree Veld as the initial stage in a Bush succession. The grass-fires prevent the trees from growing closer, and thus the present condition of things is maintained. In the Thorn Veld, where grass-fires are prevented by heavy grazing or by other means as when an area is fenced in and protected, the thorn trees and other species tend to close in and form thorn thickets. Clumps of Acacias, *Celastrus buxifolius* with *Royena* spp., etc. commonly occur even in the ordinary Thorn Veld. A second stage is represented by a closer growth with various lianes growing up in the thickets and increasing the shade. Various ferns appear in the undergrowth which becomes denser. The progression is towards the mesophytic. Were grass-fires entirely prevented, the succession would be limited only by the climatic factors. These at present are of too adverse a character to permit of high forest and it is impossible to say how far the climate would be altered by the presence of denser vegetation or how far the type would progress in the absence of fires. The different varieties of Tree Veld depend on differences, partly in climate, partly in soil conditions and partly it may be, since the area covered is so great, on the factors controlling the distribution of species, some of which may be no longer in operation.

SUCCULENT AND THORNY OR SEMI-KARROID SCRUB OF LOWER ALTITUDES

This type is found in Natal in the dry river valleys, e.g. the great valley of the Tugela. It shows connections with the more xerophytic Tree Veld but differs in being more dense and in the relative scarcity of grasses. In Natal, it consists of tree Euphorbias (*E. tirucalli*, *E. grandidens*), *Aloe* spp., *Encephalartos altensteinii* (in places), *Commiphora* spp., *Hippobromus alata*, *Rhus* spp., *Ptaeroxylon utile*, *Acacia* spp., *Mesembryanthemum* spp., with succulent or semi-succulent lianes such as *Sarcostemma viminalis*, *Dregia floribunda*, *Riocreuxia* sp., *Capparis* spp., *Secamone* sp., *Ceropegia*, *Vitis* spp., *Senecio* spp., etc. Outside Natal it occupies still greater areas. Westward, from the Kreiskama River and particularly in the district of the lower Fish River, a similar type is described by Sim (see p. 5 of "Forest Flora"). In addition to succulents, there are present in this case very much dwarfed forest species such as *Ptaeroxylon utile*, *Elaeodendron croceum*, *Apodytes dimidiata*, *Scolopia zeyheri*, *Sideroxylon inerme*, *Celastrus peduncularis*, *Schotia latifolia*, as well as others more characteristic of Succulent Scrub, *Portulacaria afra*, *Capparis albitrunca*, *Maerua triphylla*, *Pappea capensis*, *Euclea undulata*, *Olea verrucosa*, *Rhus* spp., *Royena* spp., *Celastrus* spp., *Euphorbia* spp.

According to Sim, "The shrub trees grow in clumps or thickets separated everywhere by bare paths or water runs. Viewed from an overlooking

height, the landscape shows a vast, flat, forest plain apparently dense and of unknown depth as the interspaces only show on close inspection, but a closer inspection shows that it is rather a goat-grazing country and an ostrich run than a timber forest. When the spekboom (*Portulacaria*) is in flower, its bright rosy colour pervades the scene; at all other times the landscape is dull and sombre, desolate and monotonous, the secluded resort of the koodoo, the buffalo, and the elephant." Somewhat the same class of scrub, Sim states, extends interruptedly as far up as Witmos and Bethesda, and it extends also through the Addo Bush to beyond Uitenhage. It is replaced by Thorn Veld along the river valleys above Cradock. Towards the Kat River and upper Keiskama streams, the Fish River scrub gradually merges through rather poor sneezewood and wild olive scrub into high forests of the Amatolas.

The ecological nature of this type was recognised by Sim, when he says, "Fish River Scrub is the effect of a Karroo climate on a forest vegetation." Once more, it is obvious that it represents the final phase for its own climatic habitat like sclerophyllous Fynbosch, *Leucosidea* scrub of the Drakensberg, etc. With more mesophytic climatic conditions it grades into Bush.

It is necessary here to explain why this type was not considered along with the sclerophyllous types. At first that was my intention but on reconsideration it was thought inadvisable to make it appear that the succession has always been towards the mesophytic. Succulent Scrub is essentially a valley or at least low-lying type, contrasting thus with *Leucosidea* scrub, which is a mountain type. Though it grades into Bush, there is no reason in the absence of direct evidence why it should be considered a stage in Bush succession. Retrogressive Bush might just as well be considered a stage in the Scrub succession. It cannot be too much emphasized that each is the final phase for its own habitat.

THE KARROO

This succulent and sclerophyllous dwarf-shrub type represents the effect of a dry, continental climate on Grassland. The Karroo region consists of a great, shallow basin varying in its altitude from 1800 to 2500 feet above sea level, surrounded by mountains from 4000 to 8000 feet high. The rainfall varies greatly. In the driest parts (the Gouph) it is from 3 to 6 ins. (81–150 mm.) but the Little Karroo has a higher rainfall, 5 to 14 ins. (136–354 mm.). The greater part of the rainfall takes place in the summer months. The summers are very hot and the winters cold. The soil, largely in reaction to the dry, continental type of climate, is rich in chemical salts but very dry and baked. There is seldom any water in any of the numerous stream channels.

Ecologically, Karroo is, for the most part, an open or semi-open formation but nevertheless it should be classed as veld or steppe rather than as desert, for annuals (therophytes) though they occur are not very abundant or

characteristic (vide later in the description of desert). The best general description of the Karroo that has appeared so far is that of Marloth (**15**). His excellent photographs and drawings give a good idea of the many weird growth-forms.

The Gouph (a Hottentot word, meaning empty, bald, naked or nothing) may be taken as the most typical Karroo formation. Marloth classifies the most important species according to their growth-forms as follows. (a) *Bushes and dwarf shrubs* such as *Lycium arenicolum*, *Rhigozum trichotomum*, *Pelargonium* spp., *Zygophyllum* spp., *Astephanus massonii*, *Hermannia desertorum*, *Dicoma diacanthoides* and other Compositae, *Carissa arduina* with *Viscum rotundifolium*, *Pentzia virgata*, *Walafrida geniculata*, *Galenia africana*, *Diplopappus filifolius*, *Chrysocoma tenuifolia*, *Relhania genistifolia*, *Hibiscus urens*. What is most striking is the almost total absence of green colour. "Braun ist die Farbe der Karroo." Most of the species have large root systems. (b) *Leaf succulents*, including a large number of species of *Mesembryanthemum* and *Crassula*, *Anacampseros*, *Augea capensis*, *Sarcocaulon patersonii*, *Aloe* spp., *Haworthia margaritifera*, *Gasteria disticha*, *Apicra deltoidea*. (c) *Stem succulents*, e.g. *Cotyledon fascicularis*, *Euphorbia* spp., *Stapelia* spp., *Caralluma* spp., *Hoodia gordonii*, *Trichocaulon piliferum*, *Senecio* spp., *Kleinia* spp. (d) *Plants with underground water storage*, e.g. *Asparagus* sp., *Fockea* sp., *Pachypodium bispinosum*. (e) *Bulbous monocotyledons* belonging to the orders Iridaceae, Amaryllidaceae, Liliaceae (e.g. *Buphane disticha*). (f) *Grasses*: tufts of *Aristida obtusa*. (g) *Annuals*: *Arctotis stoechadifolia* and other Compositae, *Citrallus vulgaris*; species of *Helichrysum*, *Senecio*, *Sphenogyne* and *Cenia*.

The western portion of the Great Karroo is similar in many respects to the Gouph, but contains an admixture of rhenosterbosch (*Elytropappus rhinocerotis*) and ferns (*Pellaea auriculata*, *Cheilanthes pteroides*, *Ch. induta*). In the eastern Karroo, the flats are again typical of the formation while the hills have *Aloe ferox*, *Pappea capensis*, *Carissa arduina*, *Capparis oleoides*, *Rhigozum trichotomum*, *Portulacaria*, *Encephalartos* spp., *Testudinaria elephantipes*, showing a connection with Succulent Scrub. There are also outposts of sclerophyllous, south-western vegetation, and on the higher mountains eastern types like *Kiggelaria africana*, *Buddleia salviaefolia* and *Cussonia spicata*.

In the Little Karroo, there are taller Crassulaceae, e.g. *Cotyledon fascicularis*, and over wide stretches the guarri (*Euclea undulata*) is dominant. The Touws River region shows an admixture of sclerophyllous Cape species, e.g. *Protea*, *Leucadendron*, *Erica*, *Phyllica*, *Thamnochortus*, *Willdenowia*. The Robertson Karroo is a low-lying isolated patch of Karroo, surrounded by sclerophyllous formations. The West Karroo (Bokkeveld and Roggeveld or Tanqua Karroo) is also partly typical Karroo formation but shows transitions to the Cape region.

The migratory stream-bank vegetation of the Karroo region has already been dealt with. It was also pointed out that the Fellfield, which occurs in various other regions in South Africa approaches very near to Karroo formation. In Natal, in certain places, as for instance in the valley of the Tugela below Weenen, there are bare rocky slopes with succulent and hard shrubs which might be classed as Karroo.

There is room for much further work on this interesting type. The plant succession is still unknown to us. Transitions have been noted in the above account between Karroo and sclerophyllous woodland on the western side, between Karroo and Thorny and Succulent Scrub on the southern and eastern sides. On the north, Karroo passes into Compositae Veld which it approaches in its ecological character and through it into Veld. On the eastern side, it also grades into ordinary Veld. The edaphic factors are undoubtedly of importance as well as the climatic. Not only is the soil dry, hard clay but the relatively high proportion of chemical salts, it may be suggested, may possibly be one of the main factors which determine the prevalence of the succulent habit.

“BRAK” FORMATION

Over all the arid portions of South Africa, such as the dry river valleys of the eastern side and the whole Karroo and western and central portions, the soil is, as a rule, rich in chemical salts. This is a direct result of the dry climate. Precipitation is not sufficient to leach the soil and salts accumulate. In low-lying places, there is a certain amount of seepage and subsequent evaporation leads to the formation of salt pans. The vegetation of these is distinct enough in point of both habitat and physiognomy to constitute a separate formation. *Tamarix articulata* is characteristic of such places and various halophytes such as *Salsola aphylla* (Gannabush), *S. zeyheri*, *Atriplex halimus*, *Lycium* spp., *Statice* sp. etc. Pearson (**18, 19**) makes repeated mention of such halophytic associations for the western region, and towards the north, salt pans, according to the maps, occupy large areas. The detailed study of this formation appears to offer an attractive field.

DESERT

If we classify Karroo along with Veld, there is not a very great area of actual desert anywhere in South Africa. Raunkiaer (**20, 21**) and other Danish botanists, as Ove Paulsen in his memoir on the vegetation of the Transcaspiian Lowlands (**17**), use as a test for desert, the high proportion of annuals (therophytes). In the Libyan desert this, according to Raunkiaer, is 42 per cent. while the normal for the whole world's flora is given as 13 per cent. Annuals, however, are also characteristic of regions under high cultivation where the soil is continually disturbed. In a previous paper I have shown that Natal has only 6-7 per cent. of annuals and many of these are doubtfully native. This

is only about half the normal. The other formations already described also are poor in annuals so that if we apply this test none of them can be classed as desert. The so-called Kalahari desert is to be classified not as desert, but Veld. The Namib desert in S. W. Africa is, however, probably true desert, as I am informed by Dr Pearson that the proportion of annuals in parts of it at least is relatively high. Pearson (18, 19) has made a special study of this region, and it is largely due to his researches that its flora is now becoming fairly well known. He looks upon the flora as being derived from each of the surrounding plant formations. During his last visit, he made some extremely interesting notes on the plant succession which will be included in a forthcoming paper.

Marloth visited the Lower Namib in 1909 and in his description of the vegetation (16) he distinguishes four edaphic formations—seashore, sandy plain, rocky hills and gravel-covered flats. *Salsola zeyheri*, *Acanthosicyos horrida*, *Mesembryanthemum* spp. are characteristic of the sandy plains to the south, while to the north is the well-known *Welwitschia*. On the rocky hills, the kokerboom, *Aloe dichotoma*, and several species of *Euphorbia* (*E. gummi-fera*, *E. cervicornis*), *Pteronia succulenta*, *Pituranthus aphyllus*, *Mesembryanthemum rhopalophyllum*, *Augea capensis*, *Sarcocaulon rigidum* (Bushman's candle). The central plateau, as already described, is an arid type of Tree Veld.

THE PLANT SUCCESSION ON THE COAST

The whole coast-line of South Africa except in a very few places is sandy, and the drifting sand, by invading the other formations, has produced an entirely new succession which is fairly easily determined. The sand-dunes which line the eastern side vary in height from 50 to 200 feet and have been entirely fixed by the growth of Psammophilous Bush.

In Natal, the succession is as follows. On the belt of shifting sand between the bush and the sea the following species grow and act as sand-binders: *Scaevola lobelia*, *Cyperus natalensis* (the leafy form), *Ipomaea pescaprae* (*I. biloba*), *Hydrophylax carnosa*, *Gazania uniflora*, *Mesembryanthemum edule* and the grass *Sporobolus pungens*. The actual order in succession between these varies at different spots. As soon as the sand gets partially fixed, a variety of other species come in, e.g. *Canavalea obtusifolia*, *Cryptostemma niveum*, *Passerina ericoides*, *Helichrysum teretifolium*, *Osteospermum moniliferum*, *Samolus porosus*, *Tephrosia canescens*, *Cynanchium* spp., *Brachylaena discolor*. Then follows the typical Sand-dune Bush with *Mimusops caffra* (red milkwood) dominant and a great variety of other trees such as *Scolopia zeyheri*, *Brachylaena elliptica*, *Erythrina caffra*, *Apodytes dimidiata*, *Kraussia lanceolata*, *Dovyalis rotundifolia*, *Rhus* spp., and in places *Strelitzia angusta*, *Hyphaene crinita*, *Aloe supra-laevis* and *Strychnos spinosa*. The abundance of lianes is a feature of Sand-dune Bush, while herbaceous undergrowth is

almost entirely absent. The trees composing the Sand-dune Bush are on the whole very distinct from the species found in the Coast Bush behind the dunes, though some of the sand-dune species occur at higher altitudes.

Psammophilous tree-growth is confined to the eastern coast where the climatic factors permit of it. At the Cape, the succession is different. Marloth (**15**) figures *Myrica cordifolia*, *Chymococca empetroides*, *Passerina filiformis* and *Sideroxylon inerme* as "Dünensträucher" and in one of his excellent plates shows the grass *Ehrharta geniculata* binding the sand, followed by *Mundia spinosa*, *Myrica cordifolia* and on the summit of the dunes, *Rhus crenata*. The more adverse climate of the Cape has the same effect on the sand-dune vegetation as on the other types. Instead of tree-growth we get a type corresponding to Sclerophyllous Woodland.

At the river mouths, the succession differs. In wet sandy soil where the water is not brackish we get, instead of the Sand-dune Bush, the interesting *Barringtonia racemosa*, *Hibiscus tiliaceus*, *Voacanga thousarii*, *Eugenia cordata*, etc. On mud flats at the river mouths with salt or brackish water, various halophilous species such as *Salicornia* and *Chenolea diffusa* form spreading clumps. As far south as the rivers of the Transkei (Kogha River mouth) the final stage on the mud flats is Mangrove formation. The three species of Mangrove found at Durban are *Rhizophora mucronata*, *Bruguiera gymnorhiza* and *Avicennia officinalis*. Mangrove formation increases enormously in importance as we proceed northwards along the coast of Portuguese East Africa. Sim (**25, 26**) states that it lines, with interruptions, the whole coast of that region from Delagoa Bay northwards and extends inland along the rivers for many miles. In addition to the more hardy species which form outliers in South Africa named above, the following occur: *Ceriops candolliana*, *Carapa moluccensis* (*Xylocarpus granatum*), *Lumnitzera racemosa*, *Sonneratia acida*, *Heritiera littoralis* with the fern *Acrostichum aureum* as an occasional companion.

GENERAL REMARKS

There are few countries that can show more varied types of vegetation than South Africa. There is every stage from desert and open edaphic formations, through every gradation of open, semi-open and closed Steppe, through great variety of sclerophyllous and other Scrub to a mesophytic type of Evergreen Bush, while along the coast, there are Psammophilous Bush and Mangrove types. The succession is not always towards the mesophytic as is shown by the presence of Succulent Scrub in the dry river valleys. Tree Veld of various kinds—an intermediate type between Grassland and Forest—covers enormous areas and may represent an early stage of succession to a xerophytic type of bush, which retains its present character through the influence of grass-fires.

One striking feature of the vegetation as a whole is the rarity of formations

or associations dominated by a single species. The Macchia and Heath formations, Scrub of various kinds, most of the Bush, much of the Veld and Tree Veld, the Karroo and Psammophilous Bush of the coast, are all made up of a conglomeration of species. In the closer formations masses and clumps or tussocks, consisting of half a dozen species with their branches completely intertwined and commingled are a common feature. There are, however, a few exceptions to this. In parts of the Karroo, a single species such as *Rhigozum trichotomum* or *Mesembryanthemum spinosum* may be completely dominant over a considerable area. *Anthistiria imberbis* forms pure associations over much of the Veld, and other grasses such as *Aristida* spp. are also often dominant. *Leucosidea* scrub in the Drakensberg is sometimes fairly pure, and there are a few examples of almost pure *Podocarpus falcata* bush. Parts of the Thorn Veld, too, have no other trees than Acacias.

In many cases, the fact that no single species has been able to assume dominance may be considered to point to a lack of stability in the environmental conditions, but it is doubtful if this is sufficient to explain all the facts. *Leucosidea* scrub is an unstable type and yet it is often pure. The wattle tree, *Acacia mollissima*, a native of Australia, large plantations of which are now a feature of the landscape in Natal, is quite at home and in places, e.g. in the Harding district, is spreading naturally. Among the wattle, hardly any native species is able to exist. There is no undergrowth of any kind. An introduced species therefore is apparently able to assume complete dominance, while our native species of trees are not. This, however, is not apparent in the case of introduced weeds, with one or two exceptions. The vegetation of South Africa, as a whole, is resistant to invaders. The relationship between the various types of vegetation as described above is indicated in the accompanying diagram (Fig. 19). It is meant to apply however as a whole, only to the eastern side of South Africa.

In conclusion, it is hardly necessary to state what must be very obvious, that the above sketch, even as a sketch, remains very incomplete. A general phytogeographical map of South Africa might be attempted on the lines indicated, but it could only be completed with anything approaching accuracy if those interested, who are resident in various parts of the sub-continent, were willing to cooperate.

As to the more obvious gaps in our knowledge a few of the more important may be set down. 1. An account of the Strand Association right round the coast. 2. The distribution of Fynbosch or Macchia outside the south-western region where it is the dominant type. 3. The interrelationships between Grass Veld and Karroo, with an account of the detailed succession in the latter. 4. The exact distribution of the different types of Tree Veld (Thorn Veld, *Protea* Veld, Bush Veld, etc.), and far more details regarding the controlling factors, both climatic and edaphic. 5. An account of the vegetation in salt or "brak" places in the dry interior. 6. An investigation

into the general ecological character and relationships of Succulent and Thorny Scrub. 7. An investigation into the question of how much of South Africa is to be classified as desert.

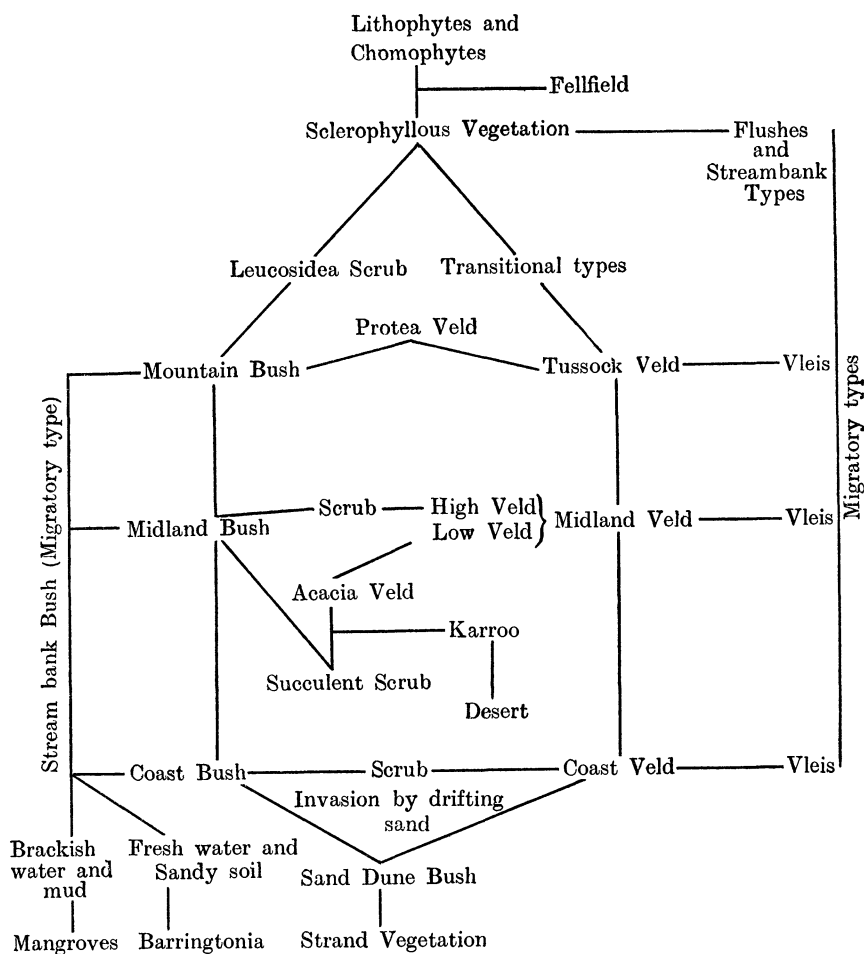


FIG. 19. Scheme showing relationships between the types of South African Vegetation described in the text.

Such contributions to our knowledge are necessary to enable us to complete a very general "primary survey" of the vegetation, without touching more intensive work, involving problems that are almost endless.

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