Fynbos ecology: a preliminary synthesis

J Day, W R Siegfried, G N Louw and M L Jarman (Editors)

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DECEMBER 1979

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PREFACE

The southern and south-western Cape is occupied by an exceptionally rich flora occurring as sclerophyllous shrublands and heathlands known locally as fynbos. The various fynbos ecosystems, their plants and animals, are of considerable scientific and aesthetic interest, while the mountain catchment areas of the Fynbos Biome are of particular economic importance both as a water resource and as recreational areas.

Much research has been conducted in the biome in the past and in order to coordinate current activities, to stimulate new research and to synthesize available scientific information within the region, the Fynbos Biome Project was initiated in 1979.

The project is one of several national scientific programmes within the National Programme for Environmental Sciences administered by the CSIR. The National Programme is a cooperative undertaking of scientists and scientific institutions in South Africa concerned with research related to environmental problems. It includes research designed to meet local needs as well as projects being undertaken in South Africa as contributions to the international programme of SCOPE (Scientific Committee on Problems of the Environment), the body set up in 1970 by ICSU (International Council of Scientific Unions) to act as a focus of non-governmental international scientific effort in the environmental field.

The first phase (1977 to 1980) of the Fynbos Biome Project has been centred on baseline studies, including the review and synthesis of current knowledge and on broad surveys of climate, soils, vegetation, fauna and land use patterns. This document brings together available information and thinking on aspects of fynbos ecology as a basis to the identification of future research needs and priorities. The second (1979 to 1982) and third (1981 to 1986) phases will concentrate respectively on detailed comparative studies of ecosystem structure and functioning and on the testing of hypotheses and models developed during the second phase.

SAMEVATTING

Die huidige stand van kennis en denkrigting oor die ekologie van die mediterreense tipe sklerofile struikveld en heideveld van die suidelike en suidwestelike kaapprovinsie word saamgevat in 13 bondige sinteses. Die Fynbosbioom word gedefinieer en gekarakteriseer in terme van flora, plantegroei-fisionomie en ekologie en die verskillende ekosisteme van die gebied word beskrywe. Klimaat- en grondvariasies en hulle verwantskap met topografie en geologie word bespreek. Die belangrikste hidrologiese en hidrobiologiese kenmerke van die gebied word aangegee met verwysing veral na plaaslike variasie in water kwaliteit. Vuur is 'n faktor van aansienlike ekologiese en ekonomiese belang in die bioom en inligting oor die voorkoms, seisoenaliteit, intensiteit en gedrag van vuur word opgesom. 'n Paleo-ekologiese perspektief word verskaf as 'n basis vir bespreking oor die gebied se biogeografie. Die plantekologie van die bioom word in detail beskryf, terwyl kort samevattings verskaf word oor dierekologie, plant-indringers en natuurbewaring. Die volume word afgesluit met kommentaar oor die beweegredes vir meer deeglike navorsing asook 'n kort oorsig van die belangrikste vrae wat prioriteit moet geniet.

ABSTRACT

Current knowledge and thinking on the ecology of the mediterranean type sclerophyll shrublands and heathlands of the southern and south-western Cape is reviewed in 13 concise syntheses. The Fynbos Biome is defined and characterized in terms of flora, vegetation physiognomy and ecology and the various ecosystems within the region are described. Climate and soil gradients and their relationships with topography and geology are discussed. The major hydrological and hydrobiological features of the region are outlined, with particular reference to local variation in water quality. Fire is a factor of considerable ecological and economic importance in the biome and information on fire incidence, seasonality, intensity and behaviour is summarized. A paleoecological perspective is provided as a basis to discussions on the region's biogeography. The plant ecology of the biome is described in some detail, while brief synopses are provided on animal ecology, invasive weeds and nature conservation. The volume is concluded with comments on the rational for intensified research and a brief examination of key issues requiring priority attention.

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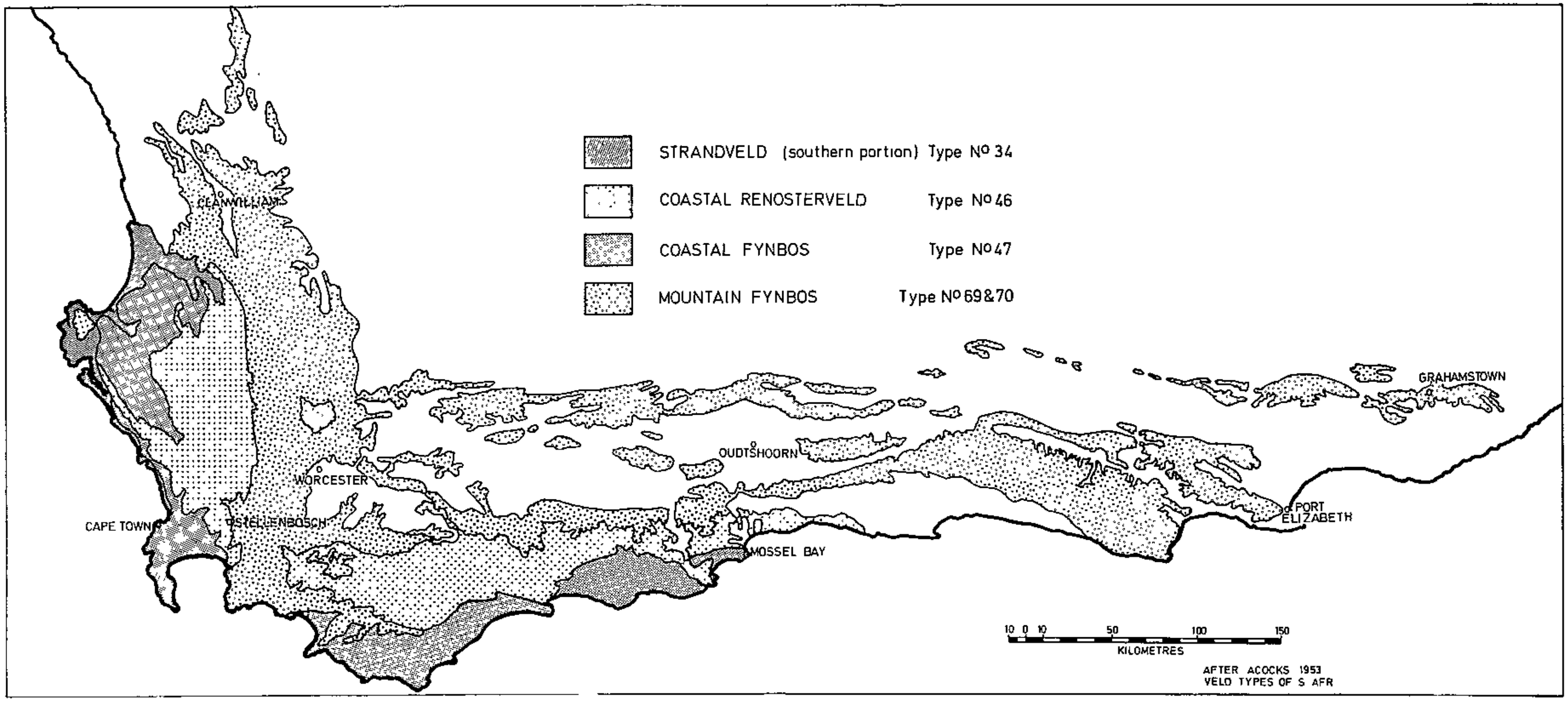

Figure 1. Map of the Fynbos Biome (from Acocks 1953)

INTRODUCTION

F J Kruger

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In the world there are five regions with a mediterranean type climate, usually characterised by cool, relatively humid winters, hot dry summers and a distinctive flora adapted to these conditions. The five regions are on the coasts of the Mediterranean, California, Chile, southern and south-western Australia, and the south-western Cape. The vegetation is commonly referred to as macchia (particularly in the Mediterranean), chaparral (California) matorral (Chile), heath (Australia), and fynbos in South Africa.

The Fynbos Biome corresponds geographically with the "Capensis" Region delimited by Werger (1978) as one of the plant biogeographic regions of southern Africa, extending roughly from 31° to 35°S and 18° to 27°E. It is characterized by the five Acocks (1953) veld types listed in Table 1. Their geographical distribution is shown in Figure 1. An adjoining veld type (no 43), Mountain Renosterveld, which is often structurally and floristically like some communities of the fynbos, is excluded by Taylor (1978) from the Capensis Region because it is ".... more akin to Karoo in habitat and floristics ...." (see also Acocks 1953). It is included by Werger (1978) among the vegetation types of the Karoo-Namib Region. Therefore, although Boucher and Moll (in press) include Mountain Renosterveld in their account of mediterranean climate shrublands, it is excluded here.

The biome is fairly well characterized by climate. Schulze and McGee (1978) show several climatic types within the boundaries of the relevant Acocks types (Table 1), but these climates have the common features of precipitation in excess of 200 mm yr^{-1} and relatively humid winters (rainfall of the three winter months in excess of about 50 mm each) which are cool but almost entirely free of killing frosts. In the west the climates are of the mediterranean or transitional mountain-mediterranean kind, with dry summers and wet winters. Eastwards the rainfall becomes increasingly non-seasonal. The range of climates is extreme. Annual rainfall, for example, ranges from 200 to 3 000 mm or more.

Acid, leached, sandy soils characterize most of the biome.

Table 1. Acocks Veld Types included in the Fynbos Biome

Type No	Name	Area[1] (km²)	Climate types[2]
34	Strandveld (southern portion)	±600	BSk, Csb
46	Coastal Renosterveld[3]	14 591	BSk, Csa, Csb
47	Coastal Macchia (Coastal Fynbos[4])	8 379	BSk, Csa, Csb
69	Macchia) 17 846) Mountain[5]	Csa, Csb	
70	False Macchia) Fynbos (False Fynbos))	17 866	Cfb

[1] As mapped by Acocks (1953)

[2] Köppen types from Schulze and McGee (1978): mountain types not identified

[3] The term "Renosterveld" is used throughout this report instead of Acocks, "Rhenosterbosveld" because the former is historically correct (C H Boucher, pers comm 1979)

[4] Coastal Fynbos is used in this work in preference to Acocks' name (see also Taylor 1978)

[5] Mountain Fynbos is used instead of Acocks' names. Included within Mountain Fynbos is a distinct sub-type, Arid Fynbos: see Taylor (loc cit) and Acocks (1953)

The relative importance of climate, substrate and biogeography in determining the form and functioning of the biome's natural communities is not yet clear but the communities share a set of peculiar physiognomic characters which distinguish them from adjoining South African biomes, and ally them with communities in mediterranean climate areas elsewhere. The main physiognomic features of the vegetation are: the prevalent sclerophyllous shrub form, the scarcity of trees, and the relatively minor importance of grasses and of evergreen succulent shrubs. Taylor (this volume) discusses various characteristic plant biogeographic features, while Cody and Mooney (1978) and Siegfried (this volume) review some of the distinctive features of the animal communities.

Included within the geographic limits of the biome, and adjoining it in parts, are forest communities of the Afromontane biogeographic region (Acocks' Veld Type 4: Knysna Forest, and allied formations). Transitions from sclerophyllous shrubland to tall evergreen broad-leafed forest are usually abrupt but not consistently marked by physiographic or biotic discontinuities. Eastwards, shrublands of the biome abut on dense thickets of Valley Bushveld (Acocks' Veld Type no 23) and similar formation types, comprising evergreen communities in which spiny trees, stem-succulent trees, and aloes are prominent. Otherwise, transitions are gradual. As the percentage of summer rainfall increases to the east, so does the relative importance of grasses, until the relationship between grass and fynbos becomes labile and the typical sclerophyllous shrub is easily eliminated, for example, by a change in fire regime (Martin 1966, Trollope 1971, Kruger this volume); this trend is reinforced if accompanied by increased silt and clay content in the soil. The gradation to open succulent or leptophyllous dwarf shrublands of the Karoo veld types is usually equally subtle (Acocks 1953 Veld Type no 5). Mountain Renosterveld (Veld Type no 43) occurs interposed between fynbos and true Karoo formations in the zone of mediterranean climate, but at the arid limits of their ranges, fynbos communities have often been so modified by certain combinations of grazing and burning that they resemble communities of Mountain Renosterveld in structure and floristic composition (Acocks 1953). Thus the boundary between fynbos and the Karoo-Namib Region is often difficult to discern. Table 2 lists the major veld types which adjoin the Fynbos Biome.

Table 2. Major Veld Types adjoining the Fynbos Biome

Type No	Name	Dominant plant formation
4	Knysna Forest	Evergreen rain forest
23	Valley Bushveld	Succulent and spiny evergreen scrub
25	Spekboomveld	Mid-dense tall succulent evergreen shrubland
26	Karroid Broken Veld	Sparse low succulent shrubland with scattered evergreen trees
31	Succulent Karoo	Sparse low succulent shrubland (variable)
43	Mountain Renosterveld	Mid-dense low semi-deciduous shrubland
44	Dohne Sourveld	Low seasonal grassland

Many plant formations occur within the boundaries of the biome, ranging from low herblands to tall scrub and open woodland. Nevertheless the constant occurrence of a distinct set of plant life forms, and the exclusive presence of a variety of less common but equally striking forms and functional features, reflect apparent adaptations which are unique in South Africa, and which show evolutionary convergence with forms and communities found in the four other distant and equally limited mediterranean climate biomes. Schimper (1903 page 507) has noted that "In all these widely separated countries the vegetation bears essentially the same stamp, in spite of deep-seated difference in composition of the flora. It is dominated by sclerophyllous plants, and always, though to a subordinate extent, by tuberous and bulbous plants." Cody and Mooney (1978) in a recent analysis of comparative data from four mediterranean climate sites, including the Cape, were able to demonstrate a "generally comparable ...." series of plant strategy-types, with sufficient consistency in ".... the adaptive relationships of leaf features to plant carbon, nutrient and water balance in the mediterranean climatic type ....." to support the hypothesis of convergence. Nevertheless the South African communities are different from those of other mediterranean climate biomes in certain important respects, notably in community diversity, plant seasonality and community structure. Intercontinental differences in plant "morphotypes" and "strategy-types" are likewise reflected in intercontinental divergences in animal forms. These divergencies between Cape mediterranean-type ecosystems and Mediterranean and New World analogues are apparent also in the comparable Australian heathlands (see, for example, Kruger 1977, Specht in press), ecosystems which, like fynbos, have soils with characteristically low nutrient concentrations.

The comparative study of these small, isolated, but strikingly similar mediterranean-type ecosystems has long been seen as an important avenue for the development of ecology. In the fields of pure science this consideration must serve as prime motivation for sustained ecological studies of the fynbos, the more so because its unique features demand explanation. In the national context there are additional, compelling reasons for research. Extensive but fundamental information is required before it will be possible to institute sound programmes for conserving the diversity of fynbos, a vegetation which is essential, as effective cover in strategically indispensable water catchments, as the recreational setting for regional and tourist populations, and as an incomparable outdoor laboratory for students and scientists. These needs are rendered all the more urgent by the steady decline in the extent and condition of the natural ecosystems due to the rapid spread of exotic woody weeds, to untimely fires and to the encroachment of urban areas, agriculture and forestry (Wicht 1945, Wicht 1971, Hall 1978, Bigalke this volume).

REFERENCES

Acocks J P H 1953. Veld types of South Africa. Memoirs of the Botanical Survey of South Africa 28, 1 - 192.

Boucher C and E J Moll (in press). South African mediterranean shrublands. In : Ecosystems of the world. Vol 11. Maquis and chaparral. R L Specht (ed). Elsevier, Amsterdam.

Cody M and H A Mooney 1978. Convergence versus non convergence in Mediterranean-climate ecosystems. Annual Review of Ecology and Systematics 9, 265-321.

Hall A V 1978. Endangered species in a rising tide of human population growth. Transactions of the Royal Society of South Africa 43, 37-49.

Kruger F J 1977. A preliminary account of aerial plant biomass in fynbos communities of the mediterranean-type climate zone of the Cape Province. Bothalia 12, 301-307.

Martin A R H 1966. The plant ecology of the Grahamstown Nature Reserve: II Some effects of burning. Journal of South African Botany 32, 1-39.

Schimper A F W 1903. Plant-geography upon a physiological basis. Clarendon Press, Oxford. 839 pp.

Schulze R E and O S McGee 1978. Climatic indices and classifications in relation to the biogeography of Southern Africa. In : Biogeography and ecology of Southern Africa. M J A Werger (ed). Junk, The Hague, pp 19-52.

Specht R L (in press). Ecosystems of the world. Vol 9. Heathlands and related shrublands. Elsevier, Amsterdam.

Taylor H C 1978. Capensis. In : Biogeography and ecology of Southern Africa. M J A Werger (ed). Junk, The Hague, pp 171-229.

Trollope W S W 1971. Fire as a method of controlling macchia (fynbos) vegetation on the Amatole mountains of the Eastern Cape. Proceedings of the Grassland Society of southern Africa 8, 35-41.

Werger M J A 1978. Biogeographical division of Southern Africa. In: Biogeography and ecology of Southern Africa. M J A Werger (ed). Junk, The Hague, pp 145-170.

Wicht C L 1945. Report of the committee on the preservation of the vegetation of the south western Cape. Special publication of the Royal Society of South Africa, Cape Town.

Wicht C L 1971. The task of forestry in the mountains of the western and southern Cape Province. Proceedings of the Grassland Society of southern Africa 6, 20-27.

CLIMATE

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INTRODUCTION

The biome is characterized by two pronounced gradients common to all climatic elements: a north-south gradient from the great escarpment (32°S) to the southern coast (34°S) and a west-east gradient from the west coast (18°E) to the south-east coast at 28°E. These gradients are superimposed on mountainous topography, giving the southern tip of Africa a mosaic of spatially diverse climates. This is illustrated by the fact that the formal climatic classifications of Köppen and Thornthwaite show a complex pattern of some ten climatic zones for the region, while a statistical grouping of rainfall stations recognizes twelve major zones with 30 sub-divisions.

AVAILABILITY OF CLIMATIC DATA

The formation of a Meteorological Committee in 1860 provided the impetus for the establishment of a network of weather stations throughout the country. Initially observations of rainfall, temperature and pressure were made at about ten stations situated between Clanwilliam and Grahamstown. With the progression of the meteorological service, records were published in report form, and today the publication by the Weather Bureau of statistical summaries of meteorological data for each year is a statutory requirement. Computerised data are also available though some are not readily accessible.

A supplementary (and complementary) network of stations is controlled by the Department of Agricultural Technical Services. Climate data are obtainable from the various regional offices of the Department; information, however, is compiled essentially for departmental usage.

Climate observations made by the Department of Forestry and the Department of Water Affairs are usually reported to the Weather Bureau and therefore data are available from the Weather Bureau files. Information recorded by the Department of Nature and Environmental Conservation in the Cape is contained in reports submitted by the stations concerned. Additional but limited data may be obtained from amateur recorders of weather conditions and from organizations such as the Botanical Society, the Wildlife Society, the Magnetic Observatory, Botanic Gardens and local councils and municipalities.

At present a standard system for the acquisition, processing and accessing of data is lacking, though urgently required. Recorded data are not presented or published in a consistent form and thus considerable effort is required to coordinate the available information.

Station classification

Although a range of climatic data is available from stations in fynbos areas, many stations record rainfall only. An analysis (Table 1) of the types of measurement made at stations reveals the scarcity of information concerning certain climatic elements.

Table 1. Estimated number of stations recording various climatic elements in the biome

Element	Stations
Rainfall	546
Evaporation	148
Temperature	120
Relative Humidity	108
Wind	71
Sunshine	69
Solar Radiation	5

In compiling a system for the classification of stations, details of the types and range of climatic elements measured at stations have been considered in preference to the number of times such measurements are made daily. Table 2 illustrates this classification system.

Table 2. Classification of stations

Station class	Elements recorded
6	Evaporation
5	Temperature + Rel Humidity
4	Rainfall
3	Temperature + Rel Humidity + Rainfall
2	Temp + Rel Humidity + Rainfall + another element (excluding Evaporation)
1	Temperature + Rel Humidity + Rainfall + Sunshine + Wind + Evaporation

Station locations

From computer print-outs of station listings prepared by the Weather Bureau and the Department of Agricultural Technical Services, an estimation has been made of the number of climate stations comprising the network in fynbos areas. Some data, usually concerning rainfall, are recorded at over 500 sites: in addition, historical data are available from a further 500 stations which are presently non-operative. Stations of classes 1, 2 and 3 total over 100 in number and are mainly situated in urban and agricultural areas, both near the coast and in the interior regions. Stations are almost invariably located at sites convenient for data collection and very few are situated in mountainous areas. Figure 1 shows the location of stations of classes 1, 2 and 3.

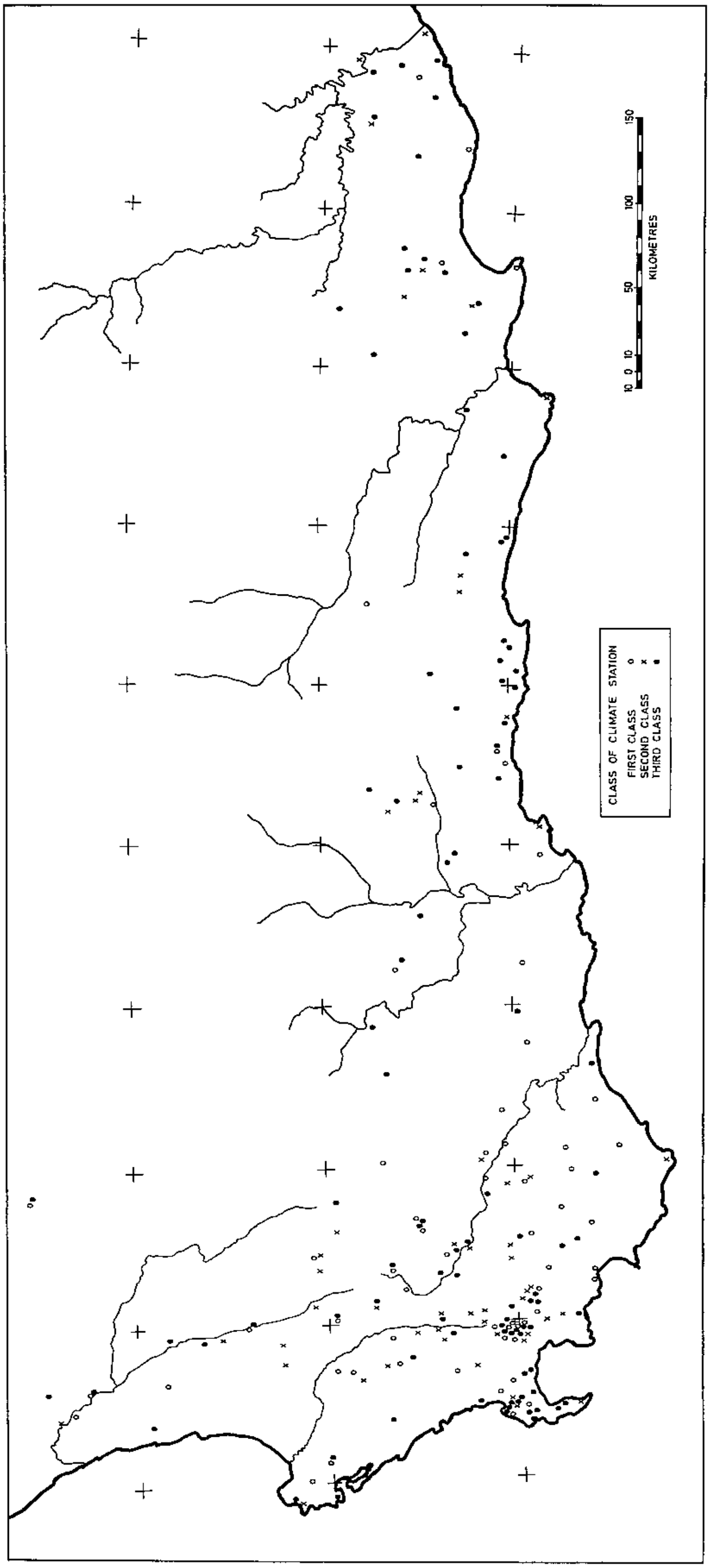

Figure 1. Distribution of climate stations within the Fynbos Biome

THE ELEMENTS OF CLIMATE

Solar Radiation

The most fundamental of all climatic parameters, solar radiation provides the basis for life and is the primary factor causing topo-climatic variations. This is due to its influence on near-surface air temperatures, on soil temperatures, on evaporation and consequently on water vapour deficit.

During summer a pronounced west to east gradient in receipt of solar radiation is found. Cape Town receives a radiant flux density in excess of 30 MJ m^{-2} day^{-1}, with a steady eastward decrease to 25 MJ m^{-2} day^{-1} at Port Elizabeth. A north-south gradient does not occur in summer and the daily receipt of solar energy is little different on north and south-facing slopes of less than 30°. In contrast, the winter pattern of solar radiation receipt shows a slight north-south gradient from 11 MJ m^{-2} day^{-1} near the south coast to 12 MJ m^{-2} day^{-1} inland. North and south-facing slopes show pronounced differences, north-facing slopes of 20° receiving 3 to 5 times as much energy as equivalent slopes facing south.

Temperature

Mean annual temperatures throughout the region are close to 17°C but the mean annual temperature range is less than 8°C in the immediate vicinity of the coast and exceeds 12°C inland. As can be expected in mountainous country, temperatures vary considerably with locality. Apart from occasional high temperatures accompanying winds on the coast, highest sustained summer temperatures (greater than 30°C) are recorded in the Great Karoo as well as in the major river basins. These locations also experience the lowest winter temperatures due to strong nocturnal infra-red radiation and katabatic drainage of cold air from the mountains to the valleys. Frost is a rare phenomenon near the coast but is the rule in July and August in the interior. For example Elgin has a frost period of 110 days per annum.

A regression of temperature decrease on altitude, performed by the South African Weather Bureau, suggests that in the mountains of the south-western Cape temperatures decrease by 0,5°C per 100 m throughout the year, while in the southern Cape mountains the rate is 0,5°C per 100 m in summer but 0,55°C per 100 m in winter. Temperature records from the mountains are, however, almost completely lacking.

Rainfall

Although the south-western and southern Cape are frequently referred to as the winter rainfall region this is a misnomer. Only the extreme south-western tip of the continent from Cape Agulhas westward experiences predominantly winter rains with a markedly dry summer. Eastward of Swellendam rain falls throughout the year, with Swellendam and Mossel Bay having rainfall maxima in spring and autumn while Port Elizabeth has rain throughout the year. A true summer maximum is first evident at East London.

The rainfall pattern is complex but closely related to topography, and depends largely on the exposure of mountain slopes to north-westerly and south-westerly winds. Additionally, mountain peaks may be cloud capped for several days, and over 500 mm of water may be precipitated per annum from wet stratus cloud without being recorded in standard raingauges. Reliable data on this subject are, however, not available.

Highest rainfall is recorded in the Slanghoek, du Toit's, Wemmershoek and Drakenstein mountains where over 2 500 mm fall per annum. This is in sharp contrast to the 400 mm recorded on the neighbouring Cape Flats and the 300 mm mean annual rainfall of Worcester, situated in a sheltered valley leeward of the mountain ranges. Along the entire southern coast the Langeberg, Outeniqua and Tsitsikama mountains separate the cloudy coast, with frequent but low rainfall, from the clear skies and dry conditions of the interior valleys. It must be stressed that the rainfall of coastal locations seldom exceeds 750 mm per annum, while the nearby mountain slopes receive double this amount and the interior valleys less than 400 mm.

Wind

The region's entire coastal belt is characterized by strong winds. West of the north-south trend of the Hottentots Holland mountains and their northern extensions, summer winds are dominantly south-east to southerly, while winter winds dominate from the north-west and south-west. Sea breezes exert an influence when gradient winds are light, appearing as shallow north-westerly to westerly air drifts along the Atlantic coast but as shallow south-easterly flows on the south coast. In summer the sea breeze over False Bay reinforces the southerly gradient winds, giving rise to maximum wind velocities in the early afternoon. It is common under light gradient wind conditions for a southerly breeze to occur over False Bay while a north-westerly breeze blows on the Atlantic coast. Land breezes are not found in the south-western Cape due to the very cold sea temperatures.

From Cape Hangklip eastwards a slight sea-breeze influence is evident throughout the year but prevailing winds are roughly east and west, changing gradually to south-east and north-east between Port Elizabeth and East London. The main difference between winter and summer winds east of Mossel Bay is the high frequency of easterly winds in summer (greater than 25%). The warm Agulhas current off the coast provides a land-sea temperature gradient sufficient for land breezes to develop on calm clear nights. Katabatic drainage down the major valleys cutting the mountain ranges reinforces the land breeze to give moderately strong off-shore winds seaward of major valleys. Morning fog is common in these valleys in winter. In the interior there is much less wind than on the coast, the percentage of calms is higher and in the west a greater westerly component is evident in both summer and winter. In the eastern interior the prevailing winds are easterly to south-easterly in summer and north-westerly in winter.

The entire littoral is subject to occasional hot desiccating gusty winds, especially in winter. These outbreaks of subsiding air heated by compression become more marked eastward along the coast. The wind blows at right-angles to the coast and is responsible for temperature rises of over $10^{\circ}C$ in a few hours. These hot dry winds play a significant role in the fire-climate of this region.

Saturation deficit and evaporation

Saturation deficit represents the amount (in millibars) by which atmospheric water-vapour-pressure falls short of saturation, and is an index of the 'evaporative power' of the atmosphere; based on both temperature and relative humidity. Saturation deficit is a good index of atmospheric water demand but is not directly proportional to evaporation as the latter is also strongly influenced by availability of energy (solar radiation) and on wind to maintain a water-vapour gradient.

At coastal locations throughout the region the mean annual 08h00 saturation deficit is close to 3 mb and the 14h00 value close to 8 mb. The mean annual saturation deficit in the intermontane valleys is about 4 mb at 08h00 but exceeds 15 mb at 14h00.

Along the southern coast the 14h00 saturation deficit shows no seasonal variation but in the south-western winter rainfall area and in the interior valleys summer deficits may exceed 30 mb. No values have been determined for mountain locations but it is likely that pronounced differences will occur on slopes of different aspect, subject to different moisture regimes and solar radiation receipt.

Actual evaporation from a Class A pan is close to 2 000 mm per annum in both the interior valleys and in the south-western Cape, with about 40% occurring in summer. Along the southern coastal areas east of Mossel Bay, annual evaporation is approximately 1 500 mm with 35% occurring in summer. No values are available for mountain locations but the same pattern as discussed for saturation deficit is likely to prevail.

CONCLUSIONS

Although it is possible to survey the broad trends apparent in the climatic mosaics of the southern and south-western Cape it must be clearly recognized that reliable data are limited to coastal recording stations and valley-floor towns in the interior. It must also be appreciated that the recording stations have been established to give a generalized picture of climatic trends and not to highlight the micro-climatic variations characteristic of the region. An expansion of stations measuring parameters of concern in biological studies has recently been undertaken by the Department of Agricultural Technical Services and the Department of Forestry, but the number of stations recording climatic data in the mountain ranges is still small.

Climate stations representative of mountain slopes of northerly and southerly aspects, as well as of mountain summits and plateaux, will be required if a full understanding is to be acquired of the climatic variability of the south and south-western Cape. Such stations should measure solar radiation, wet and dry bulb temperatures, rainfall, precipitation from cloud, evaporation, wind speed and direction, and soil temperatures. Simple, reliable equipment is available for such observations, provided the measurement sites can be visited twice daily in all weather conditions. If the latter condition cannot be met, more sophisticated and less reliable equipment will be required. The measurement of climatic conditions in important mountain locations is essential for a precise description of the climates of the Fynbos Biome.

SOURCES OF CLIMATIC INFORMATION

Jackson S P and P D Tyson 1970. Aspects of Weather and Climate over Southern Africa. In : The Standard Encyclopaedia of Southern Africa 3. D J Potgieter (ed). Nasou, Cape Town, pp 258-269.

Meteorological Services of the Royal Navy and the South African Air Force 1944. Weather on the Coast of Southern Africa, Vol 2. Cape Times Ltd, Cape Town.

Schulze B R 1965. Climate of South Africa. Part 8 General Survey WB 28. Weather Bureau, Pretoria.

Schulze R E and O S McGee 1977. Climatic Indices and Classifications in relation to the Biogeography of Southern Africa. In : Biogeography and Ecology of Southern Africa. M J A Werger (ed). W Junk, The Hague.

GEOLOGY, GEOMORPHOLOGY AND SOILS

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PHYSIOGRAPHY

Wellington (1955) has sub-divided the area occupied by the biome into two physiographic elements, each with its own distinct terrain morphology, geology and soils. These are the Cape Folded Belt and the Coastal Foreland.

The Cape Folded Belt

The biome is dominated by the Cape Folded Belt with its pronounced anticlinal folded mountain ranges, consisting mainly of hard, resistant, quartzitic rocks belonging to either the Table Mountain Group (TMG) or occasionally to the Witteberg Group, both of the Cape Supergroup (Geological Survey 1970) (Figure 1). Two main zones of folding are distinguished: a western zone with a north-south trend forming a wide arc. concave to the west, and an eastern zone running generally from west to east and curving slightly south of east. The western mountain ranges are more or less parallel north of Tulbagh, while to the south, the folding takes various directions. This is probably a result of the meeting or syntaxis of the north-south and east-west fold axes.

Three orographic lines are recognized north of the syntaxis, namely the fold ridge mountains of the Olifants River, Cold Bokkeveld and Cedarberg ranges (Figure 2). The last has a broad anticlinal structure which dies out in the north. To the east of these TMG ranges Witteberg quartzites form the Swartruggens range. The syntactic region extends in a south-westerly direction from the Hex River mountains, with peaks as high as 1 900 m, through the Du Toit's to the Hottentots Holland and Kogelberg ranges, where it ends abruptly in the sea.

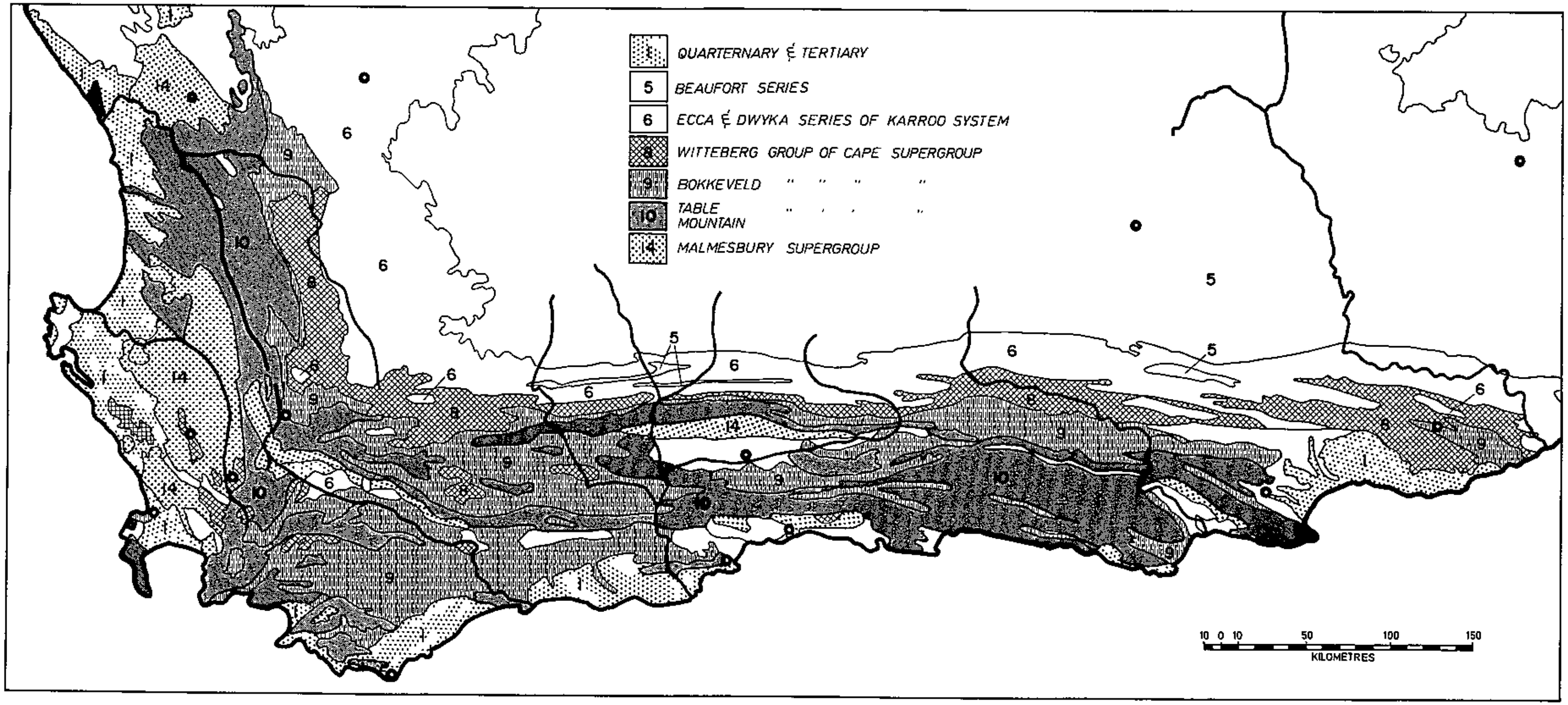

Figure 1. Geology of the Fynbos Biome

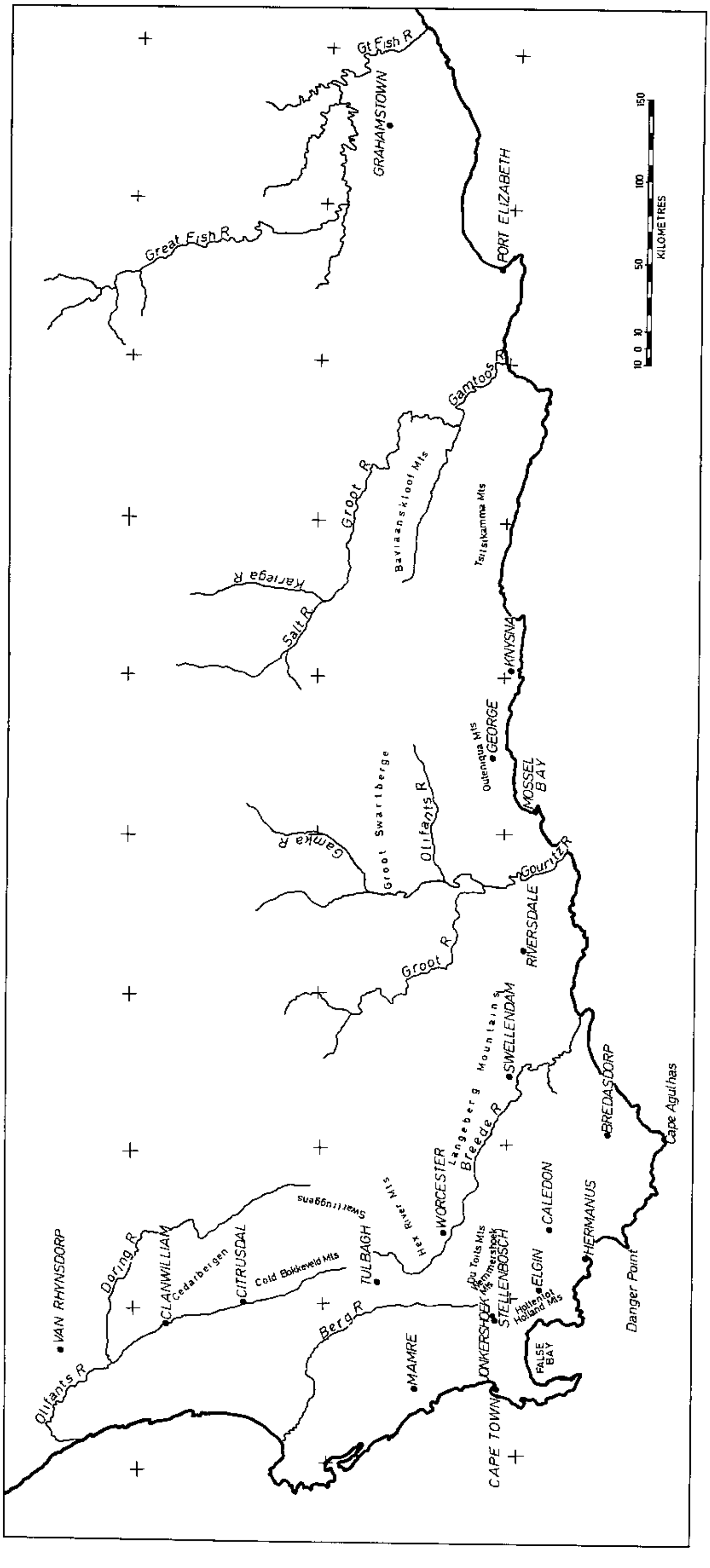

Figure 2. Map of principal localities within the Fynbos Biome cited in this volume

The eastern zone includes four main ranges with the Langeberg range forming the northern border of the southern Coastal Foreland. This range is followed, to the north, by a discontinuous line of low mountains of which Warmwaterberg is one of the bigger TMG exposures. Further north the Swartberg range, attaining a height of some 2 000 m, is followed by the Witteberg range, starting in the west at Bonteberg and grading out in the east near the mouth of the Great Fish River. Prominent features of the folded zone are the numerous synclinal and fault valleys and relatively extensive upland plains. These valleys are usually underlain by the easily weatherable slates and phyllites of the Bokkeveld Group, or occasionally by the Malmesbury Supergroup or granites, as in the case of Jonkershoek or Attakwaskloof north of Hermanus. Some of the valleys, such as those of the upper reaches of the Olifants River near Citrusdal, are very narrow, in which case locally-derived colluvial and fluvial sandy sediments from the mountain slopes cover the slates and phyllites of the valley bottoms. The valleys of the eastern zones tend to be very wide; the Little Karoo is a well known example. Of particular interest, however, are the upland plains such as the Cold Bokkeveld at 1 000 m and the Grabouw-Elgin region at 350 m, which are underlain by Bokkeveld slates. These slates are highly weathered due to the high rainfall to form clayey soil materials.

The slope characteristics of the fold zone depend largely on the lithology and structure of the underlying rock, the degree of folding and faulting and the prevailing climate. Generally the more quartzitic the rock and the drier the climate, the more rugged and steeper the slopes on highly folded zones, with bare rock faces dominating the landscape.

Coastal Foreland

The physiographic zone between the folded belt and the coast is called the Coastal Foreland. The general topography of the western foreland is that of a smoothly undulating plain underlain mainly by Malmesbury formation phyllites and with a maximum elevation of less than 200 m. Along the west coast, terminating on the Cape Flats, an old coastal plain with elevations of less than 50 m is covered by a strip of drift sand of considerable depth. In the Velddrif area the sand cover extends 50 km inland whereas it is only a few kilometers wide near Melkbosstrand.

The even plain surface is, however, broken by a number of smooth, rounded granite batholiths such as Paarl Mountain, as well as relic anticlinal TMG massifs such as Piketberg, Simonsberg and the Cape Peninsula (Geological Survey 1970).

South of the Langeberg the Coastal Foreland is also characterized by a number of discontinuous fold ridge remnants as seen near Caledon, Bredasdorp, Potberg and Hermanus. The rest of the Foreland, gradually sloping from an elevation of about 300 m at the foot of the Langeberg towards the sea, is underlain by Bokkeveld slates. To the east the Foreland is cut into TMG and forms a high coastal shelf, except for a small granite batholith near George. Particularly on TMG there are well developed remnant plains with deeply-dissected, steep-sided valleys. On the shales, however, the topography is undulating to rolling. A well developed coastal plain, covered by recent calcareous sands, limestones and local marine clays, extends from Hermanus along the coast as far as Mossel Bay. Low dune-like hills characterize the limestones while the more clayey deposits occur on flat, low-lying plains at elevations generally not exceeding 15 m.

RELATIONSHIPS BETWEEN GEOLOGY, GEOMORPHOLOGY AND THE FYNBOS

A comparison of Acocks' (1953) vegetation map with the geological map of the Republic of South Africa (Geological Survey 1970) clearly reveals a very close relationship between fynbos, physiographic subregions and geology. Macchia and False Macchia (Acocks 1953) (Mountain Fynbos in this account) are mainly restricted to the quartzitic mountain ranges and to those upland plains and valleys of the folded zone where the prevailing rainfall is sufficiently high to allow the development of moderately to highly leached acid soils on any of the more basic rock types such as granites or slates. These veld types are also found on anticlinal TMG remnants in the western and southern Coastal Foreland, as well as on some granite batholiths. Coastal Macchia (Acocks 1953), (Coastal Fynbos in this account) on the other hand, is mainly restricted to recent drift sands along the west coast and to recent calcareous sands, limestones and coastal plain soils along the south coast. North of Agulhas, Coastal Fynbos is also present on an outlier of the undulating Coastal Foreland underlain by slates, but with a much higher annual rainfall than is normal for the Foreland in this region.

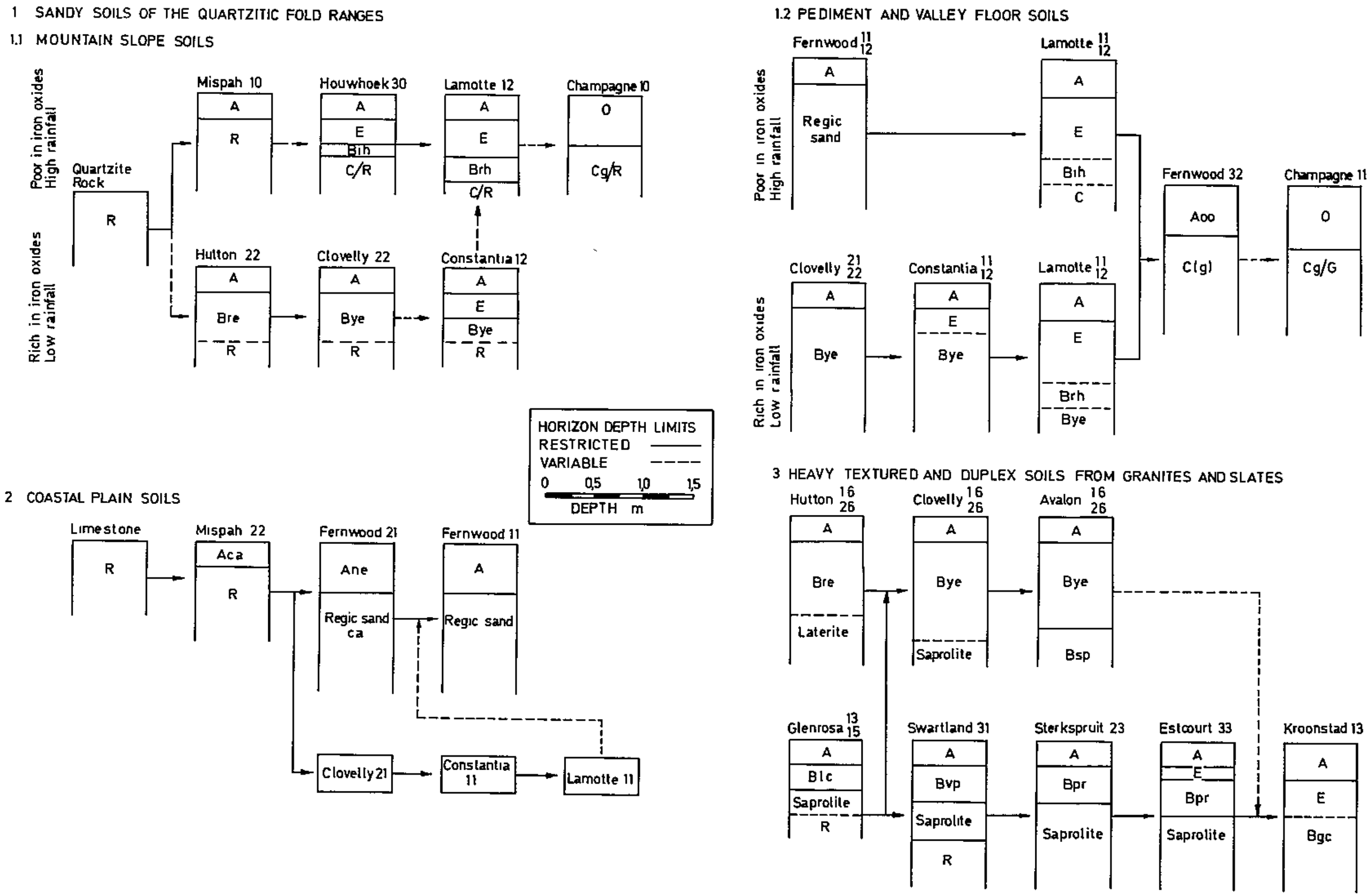

Figure 3. Soil forms, soil series numbers and slope catenas associated with fynbos. O - organic horizon; A - mineral topsoil; E - bleached subsoil; B - diagnostic subsoil; C - parent material; R - rock; G - firm gley; ca - calcareous; gc - gleyed cutanic; ih - illuvial humus; lc - lithocutanic; ne - neocutanic; oo - organic rich; pr - prismacutanic; re - red apedal; rh - illuvial iron/humus; up - pedocutanic; ye - yellow apedal

SOILS

As a result of a wide range of environmental conditions, a great variation of soil types and associations of soils is characteristic of the Fynbos Biome. A schematic outline of soil forms (MacVicar et al 1977), diagnostic features and developmental sequences of fynbos soils is shown in Figure 3. Ten broad soil associations can be recognized using parent material, rockiness, soil depth, texture and acidity as differentiating criteria (Figure 4).

Sandy soils of the quartzitic fold ranges

Soils associated with quartzitic rocks are restricted to the folded zone and anticlinal remnants on the Foreland. Due to the very hard, resistant rock type, weathering is slow and most of the weathering products of the steeper slopes are continuously removed by erosion and accumulate as pediment fan or talus slope materials of varying thickness and extent. On the steep sloping mountain ridges, especially the northern slopes of the ranges in the eastern zone, rock outcrops and very shallow lithosols predominate. Less steep slopes are generally characterized by pale-coloured, shallow, sandy soils of the well drained Mispah and Houwhoek, and poorly drained Cartref soil forms (MacVicar et al 1977). Varying amounts of stone, generally coarser than 10 mm and sometimes as large as 250 mm, are common. Shallow peaty soils (Champagne form) may develop in localized seepage spots.

The quartzites in the northern area are apparently higher in iron oxides than elsewhere in the fold zone. Because of the lower prevailing rainfall in these areas, shallow yellow to yellowish red, sandy to sandy loam soils of the Clovelly and Hutton soil forms develop on slopes. Similar soils are found locally in the higher rainfall syntactic and eastern zones but are restricted to convex upper slope positions on iron-rich strata. North of George, deep red and yellow loamy soils, developed from mixed lithological materials, occur on dissected lower slopes.

A great range of soils, all sandy, acid and highly leached (ie of low nutrient content) have developed from the pedimented colluvial and alluvial accumulation products in intra- and inter-mountain valleys. In drier areas with yellow/red upslope soils, the following catena is characteristic: deep yellow, well drained soils

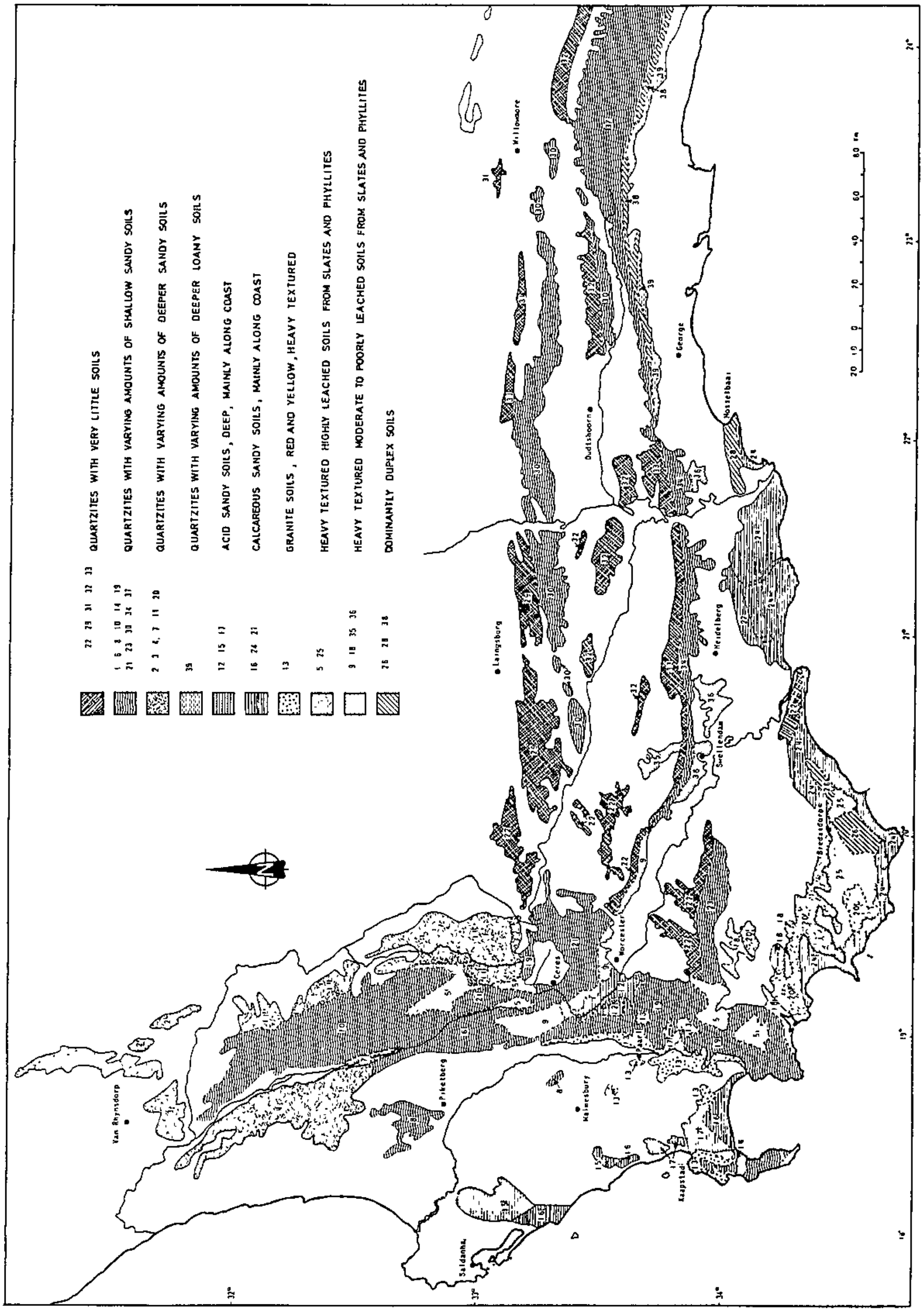

Figure 4. Soil associations of the Fynbos Biome

(Clovelly form) which gradually develop bleached A/E horizons (Constantia form) and on the lower slopes typical podzolic soils with pale coloured A/E horizons on a dark reddish brown, iron and humus illuvial B horizon (Lamotte form). In higher rainfall zones and on iron-poor parent materials, however, these soils are deep, pale sands (Fernwood form) with poorly expressed humic podzolic B horizons on the lower slopes. Although all the soils of the valley slopes appear morphologically to be well drained, Lamotte and Fernwood in particular may be subjected to various degrees of wetness during the rainy season. One of the main causes may be unweathered quartzite layers below the solum, giving rise to perched water tables. In Lamotte, wetness is sometimes manifested in a vesicular hardening of the illuvial B horizon. Along the main drainage channels the soils are generally dark coloured, and poorly drained, with abnormally high accumulations of slightly decomposed organic material. Depending on organic material content, they are classified either as wet Fernwood variants, or as Champagne form soils when containing more than 10% peaty carbon.

Heavy textured soils developed from slates, phyllites and granite

Due to their mineral-chemical composition, slates and phyllites of the Bokkeveld and Malmesbury Groups give rise to soils which differ considerably from the sandy quartzite-derived soils. They are usually heavy-textured with large fractions of fine sand and silt, and are much higher in nutrients, especially potassium. As a result of different combinations of environmental conditions three soil regions can be distinguished: upland plains, drier footslopes and duplex soil zones.

Among the upland plains, Cold Bokkeveld and Grabouw-Elgin are examples of Tertiary erosion surfaces in the folded zone, underlain by Bokkeveld slates. At present the terrain is undulating, with small remnants of the old suface. On these remnants occur deep red, highly weathered, clayey soils with varying amounts of ferruginous gravels and/or laterite. They are porous, well drained, highly leached and rich in kaolin. On the younger dissected slopes, moderate to deep yellow apedal soils, developed in slope-creep materials from the plains, are associated with soils from residually weathered slates with thin gritty colluvial surface layers. Due to the relatively high rainfall, weathering of the underlying slates is moderate. The subsoils are therefore clayey, moderate to strongly structured and red and yellow geogenic mottled in mid to upper slopes, becoming gleyed on lower concave slopes. The Glenrosa-Swartland-Sterkspruit-Estcourt-Kroonstad catena of soil forms is characteristic.

Among the drier footslopes, the upper Breë River valley and southern slopes of the Langeberg are underlain by slates and phyllites. Due to a lower rainfall compared with that of the upland plains, the degree of weathering and leaching is considerably less. The soil pattern is therefore dominated by soils with loamy, slightly acid topsoils on clayey, red and yellow, moderately blocky-structured subsoils grading into rock (Swartland form) on convex slopes. On lower concave slopes, textural differentiation with depth in the profile becomes more pronounced, as does increased structural development and poorer internal drainage (Estcourt and Kroonstad forms).

Duplex soil zones underlain by slates are found in narrow synclinal valleys such as the Langkloof. Sandy colluvial material from the quartzite mountain slopes generally covers the residual weathered slates in the valleys. The result is soils with very sandy, pale coloured upper horizons, periodically saturated with water, on gleyed, prismatic, clayey subsoils.

Granites are limited to the gentle western slopes of the southern part of the western folded zone, to numerous outcrops in the western foreland and to the Cape Peninsula. Along drier, upper, north- to north-west-facing slopes, deep, red, clayey kaolinitic apedal and well drained Hutton form soils are common. On cooler and/or moister slopes the soils are yellowish brown, grading either into granitic saprolite (Clovelly form) on steeper slopes, or into plinthic horizons on lower slopes with deep fluctuating water tables (Avalon form). Although moderately to highly leached, these soils have a much higher nutrient content than do the quartzitic soils.

Western Foreland Soils

Along the west coast the soils have all developed from recent drift sands, locally overlying more clayey fluvial deposits or residually weathered materials. The sands are highly calcareous near the coast, commonly underlain by calcrete or coastal limestone. Inland, the lime content gradually decreases until material is found similar to the quartzite weathering products of the folded ranges.

The soils along the coast can therefore vary from very shallow calcareous sandy material on limestone (Mispah form) to deep sandy calcareous to neutral sand (Fernwood form). Inland catenas include acid, sandy soils of the Clovelly, Constantia, Lamotte and Fernwood forms. Locally, duplex soils (Kroonstad, Estcourt forms) are encountered where underlying clay is within 1,2 m of the surface.

Southern Foreland Soils

Coastal Fynbos occurs on a great variety of soils in the southern Foreland. Soils similar to those of the folded ranges are found on the Potteberg and north of Pearly Beach on TMG quartzites, while Bokkeveld slates are the dominant parent material between Bredasdorp and Gansbaai. The high rainfall and low degree of dissection of the terrain has resulted in soils with a gravelly, dark-coloured sandy loam topsoil which is generally very acid, abruptly overlying a dense prismatic clay (Sterkspruit form). On lower slope positions a pale leached horizon is found above the clay (Estcourt form). Due to the high rainfall and impermeable subsoils, seasonal waterlogging in the surface horizons is common.

A strip of coastal limestones, similar to that along the west coast, is found along the coast from Hermanus to Mossel Bay, locally covered by thin deposits of acid sands. The soils are predominantly shallow and calcareous, with scattered deeper, acid, pale-coloured sands (Fernwood form).

REFERENCES

Acocks J P H 1953. Veld types of South Africa. Memoirs of the Botanical Survey of South Africa 28, 1-128.

Geological Survey 1970. Geological map of the Republic of South Africa and the Kingdoms of Lesotho and Swaziland. Government Printing and Stationery Office, Pretoria.

MacVicar C N, J M De Villiers, R F Loxton, E Verster, J J N Lambrechts, F R Merryweather, J Le Roux, T H Van Rooyen and H J von M Harmse 1977. Soil classification. A binomial system for South Africa. Department of Agricultural Technical Services, Pretoria.

Wellington J H 1955. South Africa, a geographical study. Cambridge University Press, London.

HYDROLOGY AND HYDROBIOLOGY

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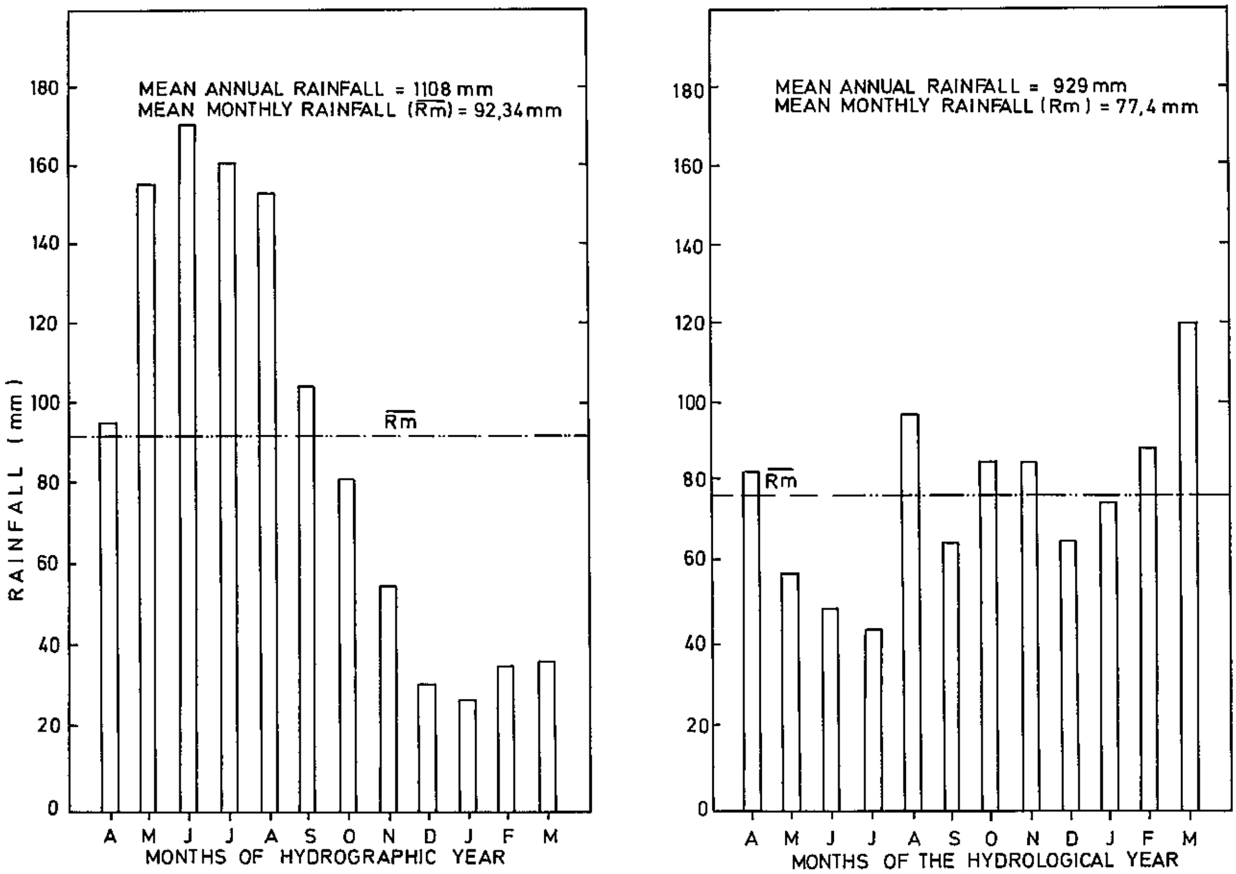
INTRODUCTION

Hydrology is the study of the water resources in the land areas of the world and hydrobiology the study of the associated aquatic biota. Water is a limited resource in South Africa, yet predictions indicate that the demand will treble by the year 2 000, with high-quality potable water accounting for "by far the greatest proportion" (Kriel 1976). At present, rivers supply almost all of South Africa's requirements and will probably continue to do so in the immediate future.

Rainfall in the western part of the Fynbos Biome falls almost entirely in winter but becomes increasingly non-seasonal towards the east (Figure 1). An additional orographic effect occurs in the mountains, giving increased runoff in rivers when thick clouds cover the upper catchments. Owing to the porous nature of the soils of the region, most of the rainwater in the mountain areas percolates into streams, and standing waters are confined to associated seepage areas or "sponges". On the flat coastal plains, most rainwater immediately infiltrates to lower levels, often into aquifers, and again there are few permanent lakes. Temporary ponds and wetlands, although never numerous, are more a feature of the seasonally arid areas of the west coast.

The principal lotic (running) and lentic (still) waters of the Fynbos Biome (Kruger this volume) are shown in Figure 2. With few exceptions, the rivers are short and steep and the lakes or pans (locally known as "vleis") are confined to the sandy coastal plains. These water bodies were originally situated largely or entirely in fynbos but agricultural and urban development have altered their surroundings to



A. MEAN MONTHLY RAINFALL : JONKERSHOEK

B MEAN MONTHLY RAINFALL : WITFONTEIN (GEORGE)

Figure 1. Average monthly precipitation for two weather stations situated in Mountain Fynbos

such an extent that the influence of fynbos on their waters can no longer be isolated except in mountain streams and a few small lakes. Here we concentrate on the untouched ecosystems while acknowledging that the others exist.

We are concerned here only with the more detailed published information. Vast amounts of raw data are stored in the records of the Department of Forestry, the Department of Water Affairs, the Department of Nature and Environmental Conservation of the Cape Provincial Administration (C P A) and the National Institute for Water Research (NIWR) of the Council for Scientific and Industrial Research.

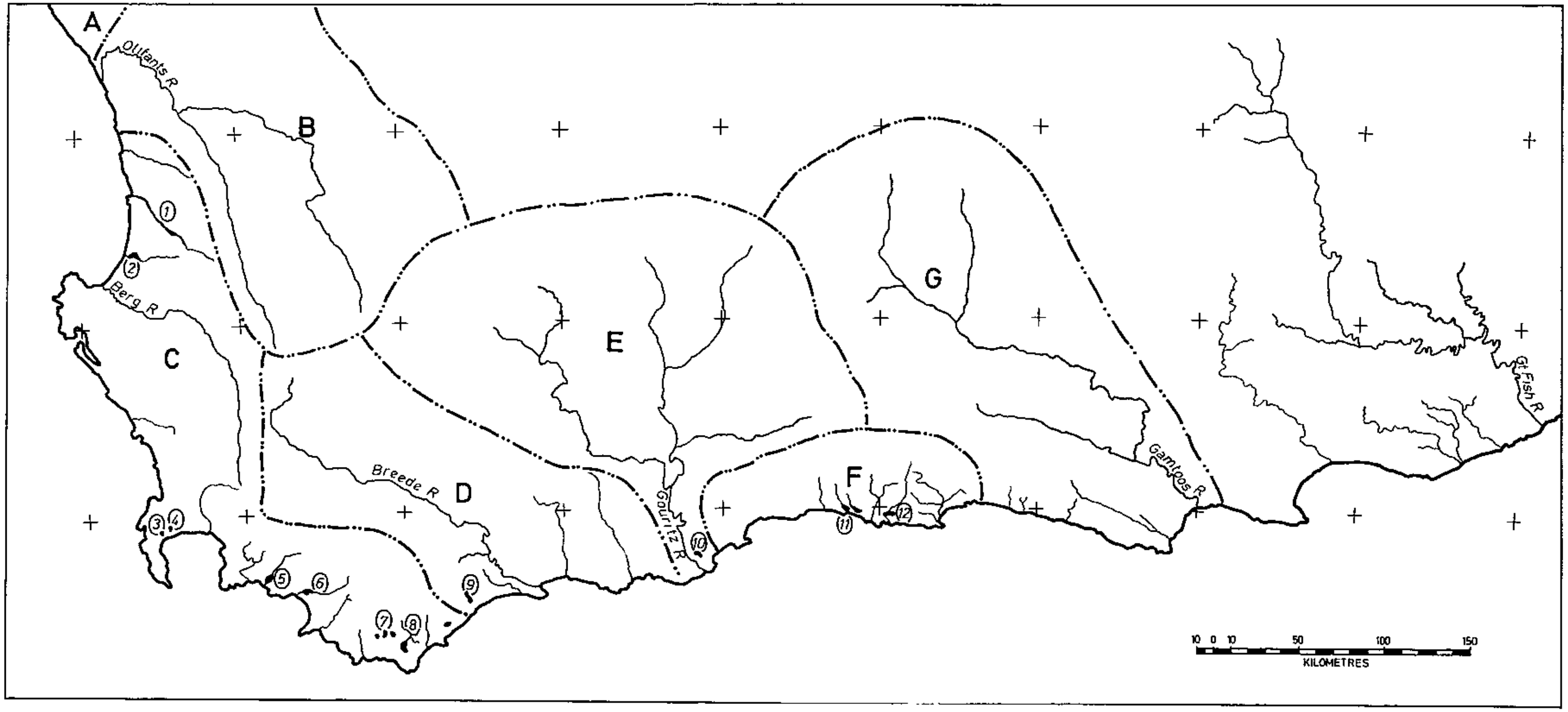


Figure 2. The principal drainage systems and standing waters within the Fynbos Biome. The contribution of the drainage systems to the South African mean annual runoff is : A - West Coast, 0,1%; B - Olifants, 2,0%; C - Berg and southwest Cape, 4,0%; D - Breede, 4,2%; E - Gouritz, 1,3%; F - Southern Cape, 1,3%; G - Gamtoos, 1,1%. The principal standing waters are : 1 - Verlorevlei; 2 - Rocherpan; 3 - Sandvlei; 4 - Seekoevlei; 5 - Bot River vlei; 6 - Klein River vlei; 7 - Bredasdorp vleis; 8 - Soetendalsvlei; 9 - De Hoopsvlei; 10 - Voëlvlei; 11 - Wilderness lakes

CHEMISTRY OF THE WATERS OF THE FYNBOS BIOME

The few reports published in scientific journals on the chemistry of the rivers of the Fynbos Biome concern the Berg River (Harrison 1958, Harrison and Elsworth 1958, Coetzer 1978a) and a number of other small rivers (Harrison and Agnew 1962). Considerably more information is available in the form of internal reports of the Cape Provincial Administration and the National Institute for Water Research. Fairly detailed data are found on the Berg River (Fourie and Steer 1971, Fourie and Görgens 1977, Fourie 1978, Hall and Görgens 1978), the Breede River (Fourie 1976, Hall and Görgens 1978) and the Eerste River (Steer 1964, Steer 1965, Steer 1966, Fourie 1978). Very little is known about lowland vleis. Published reports are available on a few small vleis in the south-western Cape (Schutte and Elsworth 1954, Harrison 1962) and on Swartvlei and Groenvlei in the southern Cape, which falls only marginally within the scope of this report. There is a single internal report on Rocher Pan in the lowlands of the west coast (Coetzer 1978b).

One feature common to all these bodies of water in their natural state is that they are oligotropic and, at higher altitudes, highly potable. This reflects low levels of nutrients in the soil (Lambrechts this volume) which are in turn reflected in the adaptations of the aquatic and terrestrial flora and fauna (King in preparation, Specht 1979, Kruger this volume, M P Hassell pers comm).

In addition to the low nutrient levels, waters of the mountain streams and high-altitude sponges have low levels of total dissolved solids (TDS), low sediment loads and are poorly buffered. Although the pH varies from river to river it seldom approaches neutrality and may be as low as 4,3. The colour is variable but often brown or "peaty", particularly on the seaward slopes of coastal mountains and to the east. In the longer rivers, TDS levels and turbidity increase in the lower reaches, resulting in a better-buffered system that is more alkaline and less brown ("white" in the literature). In low-level lakes the water tends to be white and alkaline if fed from local catchments or acid and brown if fed by mountain runoff: most of the small number of acid, brown vleis with local catchments are situated in stands of fynbos.

We have found no literature concerning the reasons for the differences in acidity and brownness of the waters of the area. The few authors discussing these factors have assumed them to be due to the presence of "humic acids" (secondary plant compounds such as tannins and other phenolics). It is known, for example, that many nutrient-poor tropical white-sand soils produce very acidic blackwater rivers rich in these "humic acids". Janzen (1974) considers the high concentrations of secondary compounds, often found in plants growing on nutrient-deficient soils, to be used by the plants as a means of chemical defence against herbivores. It would be interesting to examine the phenomenon in the fynbos region in relation to soil nutrients, particularly since browner waters have been assumed to be more acidic, yet the headwaters of the Berg River, for example, although very acid (pH 4,3 - 5,6), are not deeply stained except during spates (Harrison 1958).

In summary, then, the brownness of water is usually, but not always, correlated with pH and is more common both on the seaward slopes of mountains and in eastern rather than western regions. In the absence of further data we speculate as follows: the brown colour is due to "humic acids". These substances are leached out of decaying vegetation, particularly in sponges and vleis, and contribute to the low pH of the water. The greater the amount of water available, the greater will be the degree of leaching from plants to water. Orographic effects on the seaward slopes of mountains and the less seasonal rainfall in the east may influence the rate of leaching from decaying vegetation and thus be at least partly responsible for the geographic variation in brownness within the Fynbos Biome. Further, rainwater percolating downwards may remain for some time as ground water, accumulating leachates; during heavy rains this water would be displaced into the stream channel causing a sudden increase in colour and decrease in pH.

In the absence of adequate chemical data it is not advisable to speculate about the reasons for the strongly acidic nature of the landward-flowing white-water streams.

LENTIC WATERS

There are few unmodified bodies of standing water left in the Fynbos Biome. Many of the larger vleis are eutrophic because of agricultural runoff and urban effluents (such as Rocher Pan - Coetzer 1978b), and owing to the seasonal nature of the rainfall in the west most of the small vleis have been enlarged or deepened to form reservoirs.

Lentic waters in South Africa have been classified by Noble (1974) and Noble and Hemens (1978). Table 1 shows the types of standing waters found in the fynbos region. The influence of fynbos is evident only in the case of restio marshes, seasonal wetlands, salt pans and acid blackwater lakelets, all of which are discussed below.

Nothing is known about reedswamps or floodplains.

Marine domination of saltmarshes is almost complete and these systems are the province of estuarine rather than freshwater biologists. A great deal of information is available on saltmarshes but will not be discussed here.

Other than the blackwater lakelets, coastal lakes are not discernably influenced by fynbos; the moderately alkaline Groenvlei has been studied by Martin (1956) and Coetzee (1978), the strongly alkaline Princessvlei and Seekoevlei by Harrison (1962) and Rocher Pan by Coetzer (1978b). There is no published information on Verlorevlei and other west coast vleis with occasional seawater input.

The estuarine lakes of the southern Cape, such as Swartvlei, have been studied by the Institute for Freshwater Studies at Rhodes University. Information is available on their origin (Hill 1975), nutrients (Howard-Williams 1977, Howard-Williams and Davies 1979), primary productivity (Robarts 1973, Robarts 1976, Howard-Williams 1978), zooplankton (Coetzee 1976) and trace metals (Watling 1979).

Fynbos-dominated wetlands and vleis

The restio marshes grade imperceptibly into the sponges at river sources. Both are important and little-known ecosystems which need attention because of their influence on water quality.

The nature of the vegetation surrounding the Cape seasonal wetlands and salt pans determines the amount and type of detritus that they receive, largely in the form of wind-borne plant matter and faeces. This in turn determines the available nutrients, while the pH and concentration of ions depend both on the vegetation and on the prevailing soil types in the region. Nothing has been published on either type of system except for a few taxonomic papers on the lower crustaceans (Sars 1896 and later, Barnard 1929).

Table 1. Types of lentic inland water systems in the Fynbos Biome (partly after Noble and Hemens 1978).

Type of ecosystem	Physical Characteristics	Characteristic flora	Characteristic fauna	Examples	Degree of influence of fynbos
Vleis and floodplains					
Restio marshes	perennially waterlogged, may accumulate peat	Restionaceae, sedges	unknown	edges of source of Berg River	strong - restios dominate
Reedswamps	permanent, very shallow	*Phragmites*	unknown	inlet of stream to Bot River Vlei	weak[1]
Cape seasonal wetlands and ponds	pools filling in winter from rain or stream overflow	unknown but largely microflora	lower crustaceans including phyllopods, some insect larvae	scattered on Cape Flats	moderate when nutrients derived from wind-borne fynbos detritus
Saltmarshes	saline tidal sand- and mudflats	*Spartina*, *Zostera*, *Juncus*, Chenopodiaceae	estuarine	Langebaan Lagoon, mouths of Olifants, Berg, Breede Rivers	virtually none
Floodplains	areas inundated by floods in lower reaches of rivers	unknown	unknown	lower reaches of Gamtoos and Olifants Rivers	unknown
Endorheic salt pans	usually dry, saline when wet	unknown but largely microflora	lower crustaceans including phyllopods	occasional small pans in region of Cape Agulhas and Bredasdorp	moderate when nutrients derived from wind-borne fynbos detritus
Coastal and estuarine lakes					
Coastal lakes with no seawater input	blackwater acid (pH 5,6 - 6,6) lakelets with no marine influence	*Typha*, *Scirpus*	insect larvae; no snails; relict marine isopods	Betty's Bay lakelets, Sirkelsvlei	strong - inflow from mountain streams or stands of undisturbed fynbos
	green or white alkaline (pH 8,3-8,9) lakes with minimal marine influence	*Typha*, *Scirpus*, *Phragmites*	insect larvae; no snails; relict marine isopods	Groenvlei, De Hoopvlei	weak[1]
	green or white strongly alkaline (pH 7,4 - 12,5) lakes with minimal marine influence	*Typha*, *Phragmites*, *Potamogeton*	insect larvae; snails; no relict marine isopods	Princessvlei, Rocher Pan, Seekoevlei	weak[1] or none - on sanddunes encroached by acacias
Coastal lakes with occasional seawater inflow	fresh to brackish with minimal marine influence	*Phragmites*, *Myriophyllum spicatum*	insects typical of still inland waters with some relict estuarine fauna	Verlorevlei and other west coast vleis	weak[1]
estuarine lakes	brackish to highly saline with dominating marine influence	*Spartina* and other saltmarsh flora; *Potamogeton* in less saline regions	largely estuarine	Sandvlei, Wilderness Lakes, Swartvlei	weak - estuarine influence dominates

[1] Quality of water largely altered by agricultural encroachment on natural vegetation.

The salt pans are few and seem to be unimportant in the overall ecology of the area, but the seasonal wetlands are visited by large numbers of birds (Cooper, Summers and Pringle 1976) and appear to be important winter feeding grounds. These seasonal wetlands are threatened in a number of ways. Many small temporary ponds are being filled in and built upon while others have been obliterated by encroaching acacias; the year-round inflow of purified sewage effluent into the Kuils River has turned several temporary vleis on the Cape Flats into permanent bogs; other vleis have been enlarged to form reservoirs on farms and often receive effluents from farm drains. We urgently need to know more about the remaining natural seasonal wetlands.

The tiny blackwater lakelets and their feeder streams in the region of Betty's Bay (Black Bass Vlei, Malkopsvlei, Grootvlei) and on the Cape Peninsula (Sirkelsvlei near Cape Point) are strongly influenced by the mountain and coastal fynbos in which they are situated. A single paper by Harrison (1962), containing all the published information which exists, is briefly paraphrased below. The lakelets at Betty's Bay were formed by the "damming effect of a low coastal range of overgrown sanddunes" and Sirkelsvlei lies in "an area of small gradients and indecisive drainage". All are small and lie on narrow coastal plains unsuitable for agriculture and are therefore almost undisturbed. The water is acid (pH 5,6 - 6,6) and strongly stained with "humic acids". Phytoplankton is minimal but the marginal vegetation is well-developed (see Table 1). Insect larvae are common, as are several species of cladoceran, ostracod and peracarid crustaceans. Snails have not been found, presumably due to the combined effect of low Ca^{++} levels and low pH on the calcification of their shells. The fauna is, however, not confined to these acid or still waters and is related to that of nearby running streams.

These lakelets offer an excellent opportunity for studying the relationships between fynbos and standing waters since they are small, of easy access and are less disturbed by human activity than most other lentic systems in the fynbos.

LOTIC WATERS

The principal drainage systems of the area are shown in Figure 2. Although their estuaries stretch over a third of South Africa's coastline, the rivers contribute only 14% of the country's total mean annual runoff, reflecting primarily the relatively low mean annual rainfall of the area (Noble and Hemens 1978).

Little published information exists on the hydrology and hydrobiology of the rivers or on the extent of pure fynbos within the catchments. It is known that several rise in high altitude sponges where the waters are acid and often darkly stained, and where peat may be present. Vegetation in the sponges consists mainly of Restionaceae and Bruniaceae with a variety of other angiosperms (Noble and Hemens 1978).

Generally the upper reaches of the rivers are steep, fast-flowing mountain streams running through Mountain Fynbos, whilst their lower reaches pass through land disturbed in a variety of ways, and where many factors affect the quality and quantity of the water. There are a few very short rivers, such as the Rooiels, which descend steeply through undisturbed fynbos to their estuaries but nothing is known about them.

The rivers are usually divided into those with clear, white, slightly acid waters such as the Olifants, Berg, Eerste and Breede and those with dark, very acid waters such as the Palmiet and Storms (Harrison and Agnew 1962, Noble and Hemens 1978). Generally the white rivers are longer with well-developed zones (mountain source, mountain stream, foothills, lower river and estuary) whilst the dark rivers change abruptly from mountain stream to estuary, reflecting their origins in coastal hills and their proximity to the sea.

In the mountain streams, marginal vegetation (that in contact with the water) is scarce and consists mainly of the palmiet (Prionium serratum) and Scirpus spp. The moss, Wardia hygrometrica, occurs on boulders, and algae typical of fast-flowing waters, such as Oedogonium sp and Stigeoclonium sp, are present but not obvious. Plankton of any kind is scarce. The aquatic invertebrates are typical of fast-flowing cold waters and whilst some may be absent from the most acid streams, none appears to be restricted to them (Harrison and Agnew 1962).

The indigenous fish fauna is dominated by cyprinids and exhibits a high degree of endemism. Seven fish species are endemic to the Olifants River system and fifteen to the fynbos area as a whole (Gaigher in prep). These fifteen species represent almost 80% of the indigenous species in the area if eels are excluded and they are generally confined to the upper parts of river systems in clear, oligotropic waters. The distribution of fish in Cape rivers has not been systematically surveyed despite the fact that the indigenous fish are increasingly threatened by introduced exotic fish and by changes in the river systems.

The scarcity of green plants as primary producers in the mountain streams has resulted in an aquatic food chain based largely on plant detritus of terrestrial origin. Detritivores are common amongst the aquatic invertebrates and these feed on decaying fynbos leaves on the riverbed. Less leaf litter falls from fynbos than from stands of deciduous trees in the lower river (King in prep) and much of that which falls into the mountain stream is carried downstream by the strong currents before it can settle on the river bed. Those leaves that do settle decay slowly because of their tough, sclerophyllous nature and because organisms causing decay are rarer in nutrient-poor than in nutrient-rich waters (Kaushik and Hynes 1971). Whether the animals feed on the leaves or on the fungi and bacteria, their food appears to be more limited in the mountain streams than in the enriched waters downstream where the banks are lined with deciduous trees. It has been shown that an ephemeropteran detritivore, Castanophlebia calida, grows more slowly and is smaller at maturity in the mountain stream/fynbos section of the Eerste River than in its lower reaches (King in prep). This tendency to low productivity in the clean mountain waters seems to be reflected in most of the aquatic invertebrates and thence through the carnivores of the ecosystem.

Most of the rivers change markedly in their physico-chemical character after leaving the mountains. Generally, nutrients, turbidity and pH increase, while flow may be poor in the lower reaches, especially in the summer in the western rivers where water is extracted for human use. The quality of the water is so altered that any residual influence of fynbos is undiscernable in these lower reaches, and they will not be considered here.

Effects of Mountain Fynbos on stream water

In high-altitude regions where mountain streams flow through stands of pure fynbos, the interrelationships between fynbos and water should be most obvious. As yet, information on the hydrological processes in these areas is sparse.

In any catchment area some precipitated water is vapourized as a result of interception and evapotranspiration by the plants and most of the remainder appears as streamflow. Catchments are in fact areas of vapour loss and the management of mountain catchments consists mainly of manipulating the vegetal cover to improve water yield (Wicht 1971). Generally forested land vapourizes more moisture than does non-forested land, and afforestation of fynbos areas with Pinus radiata has appreciably reduced streamflow while veld burning or removing riparian fynbos has increased streamflow and reduced vapour losses (Wicht 1971).

Wicht (1974) has estimated that with an annual rainfall of 1 500 mm, protected Mountain Fynbos would evapotranspire 900 mm (60%) and produce a runoff of 600 mm (40%), and the streamflow : rainfall ratio in different areas of mountain fynbos has been given as 63 - 85% (Van der Zel and Kruger 1975) and 55% (Wicht 1971). The average streamflow : rainfall ratio for South Africa is 9%.

It seems that there is a relationship between the presence of fynbos in upper catchment areas and the presence of streams. The high-quality water in the streams is a valuable commercial commodity which is already being extensively exploited. Dams exist on several rivers and others are in the planning or construction stages, but their ecological effects on the rivers downstream have not been considered. The impoundments created are often stocked with fish although no information is available on their potential food supplies. The effects of both dams and introduced fish on the indigenous fish with limited ranges are unknown. With the demand for potable water increasing exponentially, the untouched ecosystems in the rivers' headwaters are becoming increasingly threatened.

FUTURE RESEARCH

A better understanding of the hydrological and hydrobiological processes in the fynbos area will require multidisciplinary research efforts. We feel that the establishment of a central data bank and of reference collections of both literature and of organisms are of prime importance in avoiding replication of research effort and in increasing efficiency. In this respect the synthesis and publication of the vast quantities of raw data in Departmental records and internal reports should be undertaken immediately. The lack of local taxonomists working on freshwater organisms, particularly invertebrates, is serious; encouragement of new taxonomists is essential.

Future work should be directed in two main lines :

1. Furthering the general knowledge of all water bodies in the area. This would include :

   - Studies of little-known ecosystems such as sponges, blackwater lakes, reedmarshes and floodplains and particularly those most threatened, such as seasonal waters and salt pans.

   - Investigation of the upstream and downstream effects of dams on rivers.

   - Tracing distribution patterns of aquatic organisms and identifying communities and habitats, particularly those that are threatened.

   - Investigations of the effects of urbanization, agricultural practices, encroachment of alien vegetation and recreational activities.

   - Tracing foodchains, estimating primary and secondary productivity of aquatic organisms and relating these to the chemical and nutrient status of the water.

2. Investigations of the particular relationships between Mountain Fynbos and water, particularly :

   - Tracing the occurrence and movement of rainwater on the surface, in the soil, as groundwater and in aquifers and streams, and determining how this is affected by the nature of the vegetation, the soil types and the geological formations of the catchment areas.

   - Examining the interrelations between the nutrient cycles of the soil, water and fynbos.

   - Determining the relationship between pH, colour and "humic acids" and the ways in which geological formation, soil, vegetation and aspect influence these variables.

- The quality and quantity of waters from areas of Mountain Fynbos. This is a high-priority project. Wicht (1971) states that "plants are man's most serious competitors for an adequate water ration and it has become as essential to check the vaporization drain of water to the atmosphere by manipulating vegetation as it is to reduce the flow of water to the sea by building reservoirs". Sufficient vegetation must remain on mountain slopes to prevent erosion and thus maintain the high quality of the water in the streams, but it is possible that the veld management of Mountain Fynbos will be designed to produce the maximum amount of high-quality water with little or no regard to, or knowledge of, its effect on the integrity and uniqueness of the flora. We urgently need to identify the point at which maximum water yield is accompanied by minimal damage to the fynbos.

REFERENCES

Barnard K H 1929. Contributions to the crustacean fauna of South Africa. No 10. A revision of the South African Branchiopoda (Phyllopoda). Annals of the South African Museum 29 (5), 181-270.

Coetzee D J 1976. 'n Ekologiese studie van die soöplankton van Wildernismere. Report to the Department of Nature and Environmental Conservation of the Cape Provincial Administration, 58-67. Typescript.

Coetzee D J 1978. A contribution to the ecology of the zooplankton of the Wilderness Lakes. PhD thesis, Stellenbosch University.

Coetzer A 1978a. The invertebrate fauna and biotic index value of water quality of the Great Berg River, Western Cape. Journal of the Limnological Society of southern Africa 4(1), 1-8.

Coetzer A 1978b. The limnology of Rocher Pan, Western Cape, with emphasis on the major Entomostraca. Department of Nature and Environmental Conservation of the Cape Provincial Administration, Report, 1-14. Typescript.

Cooper J, R W Summers and J S Pringle 1976. Conservation of coastal habitats of waders in the south-western Cape, South Africa. Biological Conservation 10, 239-247.

Fourie J M 1976. Mineralisation of western Cape Rivers: an investigation into the deteriorating water quality related to drainage from cultivated land along selected catchments, with special reference to the Great Berg River. PhD thesis, Stellenbosch University.

Fourie J M 1978. Pollution survey of rivers in the western Cape. National Institute for Water Research, Report, 30 pp. Typescript.

Fourie J M and A H M Görgens 1977. Mineralization studies of the Berg River. (1974-1976). National Institute for Water Research, Report, 30 pp. Typescript.

Fourie J M and A G Steer 1971. Water quality survey of the Berg River for the period 1963 to 1970. National Institute for Water Research, Report, 80 pp. Typescript.

Hall G C and A H M Görgens 1978. Studies of mineralization in South African Rivers. South African National Scientific Programmes Report 26, 1-24 pp.

Harrison A D 1958. Hydrobiological studies on the Great Berg River, Western Cape Province. Part II. Quantitative studies on sandy bottoms, notes on tributaries and further information on the fauna, arranged systematically. Transactions of the Royal Society of South Africa 35, 227-276.

Harrison A D 1962. Hydrobiological studies on alkaline and acid still waters in the Western Cape Province. Transactions of the Royal Society of South Africa 36(4), 213-244.

Harrison A D and J D Agnew 1962. The distribution of invertebrates endemic to acid streams in the western and southern Cape Province. Annals of the Cape Provincial Museums 2, 273-291.

Harrison A D and J F Elsworth 1958. Hydrobiological studies on the Great Berg River, Western Cape Province. Part 1. General description, chemical studies and main features of the flora and fauna. Transactions of the Royal Society of South Africa 35(3), 125-226.

Hill B J 1975. The origin of Southern African coastal lakes. Transactions of the Royal Society of South Africa 41(3), 225-240.

Howard-Williams C 1977. The distribution of nutrients in Swartvlei, a Southern Cape coastal lake. Water South Africa 3(4), 213-217.

Howard-Williams C 1978. Growth and production of aquatic macrophytes in a south temperate saline lake. Verh int Verein theor angew Limnol 20(2), 1153-1158.

Howard-Williams C and B R Davies 1979. The rates of dry matter and nutrient loss from decomposing Potamogeton pectinatus in a brackish south-temperate coastal lake. Freshwater Biology 9, 13-21.

Janzen D H 1974. Tropical blackwater rivers, animals and mast fruiting by the Dipterocarpaceae. Biotropica 6(2), 69-103.

Kaushik N K and H B N Hynes 1971. The fate of the dead leaves that fall into streams. Archive für Hydrobiologie 68(4), 465-515.

Kriel J P 1976. Interactions in water resources development. In : Resources of Southern Africa - Today and Tomorrow. G Baker (ed). Proceedings of a conference held by the Associated Scientific and Technical Societies of South Africa at Johannesburg.

Martin A R H 1956. The ecology and history of Groenvlei. South African Journal of Science 52(7), 187-192.

Noble R G 1974. An evaluation of the conservation status of aquatic bistopes. (A "Project Agua" publication). Koedoe 17, 71-83.

Noble R G and J Hemens 1978. Inland water ecosystems in South Africa - a review of research needs. South African National Scientific Programmes Report 34, 150 pp.

Robarts R D 1973. A contribution to the limnology of Swartvlei: the effect of physical-chemical factors upon primary and secondary production in the pelagic zone. PhD thesis, Rhodes University.

Robarts R D 1976. Primary productivity of the upper reaches of a South African estuary (Swartvlei). Journal of Experimental Marine Biology and Ecology 24, 93-102.

Sars G O 1896. On some South African Entomostraca raised from dried mud. Skr Videnskseksl Christiana 1895(8), 1-56.

Schutte K H and J F Elsworth 1954. The significance of large pH fluctuations observed in some South African vleis. Journal of Ecology 42(1), 148.

Specht R L 1979. Ecosystems of the world. Vol 9. Heathlands and related shrublands. Elsevier, Amsterdam.

Steer A G 1964. Pollution survey of the Berg and Eerste River. Intensive survey of the Eerste River. National Institute for Water Research, Progress Report no 2. Typescript.

Steer A G 1965. Pollution survey of the Berg and Eerste River. Monthly survey of the Eerste River. National Institute for Water Research, Progress Report no 11. Typescript.

Steer A G 1966. Pollution survey of the Eerste River including the Krom and Plankenbrug Rivers. National Institute for Water Research, Report. Typescript.

Van der Zel D W and F J Kruger 1975. Results of the multiple catchment experiments at the Jonkershoek Research Station, South Africa. 2. Influence of protection of fynbos on stream discharge in Lang River. Forestry in South Africa 16, 13-18.

Watling R J 1979. The distribution of trace metals in the Wilderness Lakes. Water South Africa 5(1), 1-13.

Wicht C L 1971. The influence of vegetation in South African mountain catchments on water supplies. South African Journal of Science 67(3), 201-209.

Wicht C L 1974. Timber and water. South African Forestry Journal 85, 3-11.

FIRE

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INTRODUCTION

The phenomenon of fire in natural ecosystems, and its use in land management, provokes considerable controversy, no doubt because it has not yet been the subject of much serious study and also because of the ambivalence so characteristic of human response to fire. Fire in fynbos has induced the usual argument, as set out below (see Wicht and Kruger 1973). It was perceived as a hazard to life and property from the earliest days of European settlement; a law of 1687 concerning unauthorised veld burning imposed "a severe scourging" for a first offence and the death penalty for the second (Botha 1924). It seems that until recently this was the dominant official attitude, at least in regard to property and cultivated lands. On the undeveloped lands of both the lowlands and the mountains the European pastoralist apparently learnt from his aboriginal predecessors (by then also his herdsmen) to use fire in extensive veld management (Kolbe 1727, Sparrman 1786 and Thunberg 1795, in Wicht and Kruger 1973). Burrows (1952), for example, quotes from written instructions of a Bredasdorp farmer in 1817, to his overseer, in which annual burning (probably patch-burning) for pasturage is prescribed. Land management in the mountains was not of great concern in the earliest years, but pastoralist practices came to official notice as long ago as the 1820's, when William Alexander reported the deleterious effects on Widdringtonia cedarbergensis of veld-burning, among other things (Alexander 1838). Pappe, then Colonial Botanist, (Pappe 1855 and later reports) and his successor J C Brown (1887) condemned veld-burning in Cape mountains as an ecological disaster, and these opinions are echoed among scientists and officialdom to this day, in spite of differing informed opinions of their contemporaries (e g Wicht 1945). See Wicht and Kruger (1973) for a review.

From an economic point of view, fire in fynbos is an important regional problem as a hazard to life and property, and because certain regimes in combination with grazing can result in environmental degradation. Under severe conditions fires may become major natural disasters, as in the series of fires in the southern Cape in 1869 (Brown 1875), or in the Betty's Bay fire of February 1970, when 21 houses were destroyed. The prolific response of invasive weeds to fire is in itself a major problem, causing expenditure of hundreds of thousands of rands annually (Taylor 1969, Hall this volume).

Protection against fire is costly; the Department of Forestry spent nearly R900 000 or 48% of its fire protection budget on protection of plantations and mountain catchments in the fynbos zone in 1977/78 (Department of Forestry, Annual Report 1977/78). The cost of protection of plantations against fire in the fynbos zone is nearly 20% greater than in grassland and savanna zones. However the cost per hectare of accidental fires in plantations in fynbos areas is 30% higher.

The phenomenon is also an ecological problem, in that the incidence of fire is a natural result of the characteristic features of the ecosystem, and that the dynamic and other functional attributes of the natural communities interact with the fire regime. Thus, for example, species like Orothamnus zeyheri cannot complete their life cycles in the continued absence of fire. Conservation is therefore at least partly dependent on the use of fire as a management tool.

In spite of the magnitude and long duration of the fire control problem, and in spite of the controversy surrounding the question, the phenomenon of fire in fynbos has not yet been the subject of any comprehensive, sustained inquiry and modern accounts are hampered by lack of basic data. In this account I shall attempt a description of fire in fynbos by reviewing available information on fire regimes.

SOURCES OF IGNITION

Figures 1 and 2 depict some data on the causes of fires in the Fynbos Biome. These are derived from Department of Forestry fire reports and although it is often difficult to determine the cause of a fire with certainty, it is also true that foresters are conservative in this respect and report large numbers of fires as being of unknown origin.

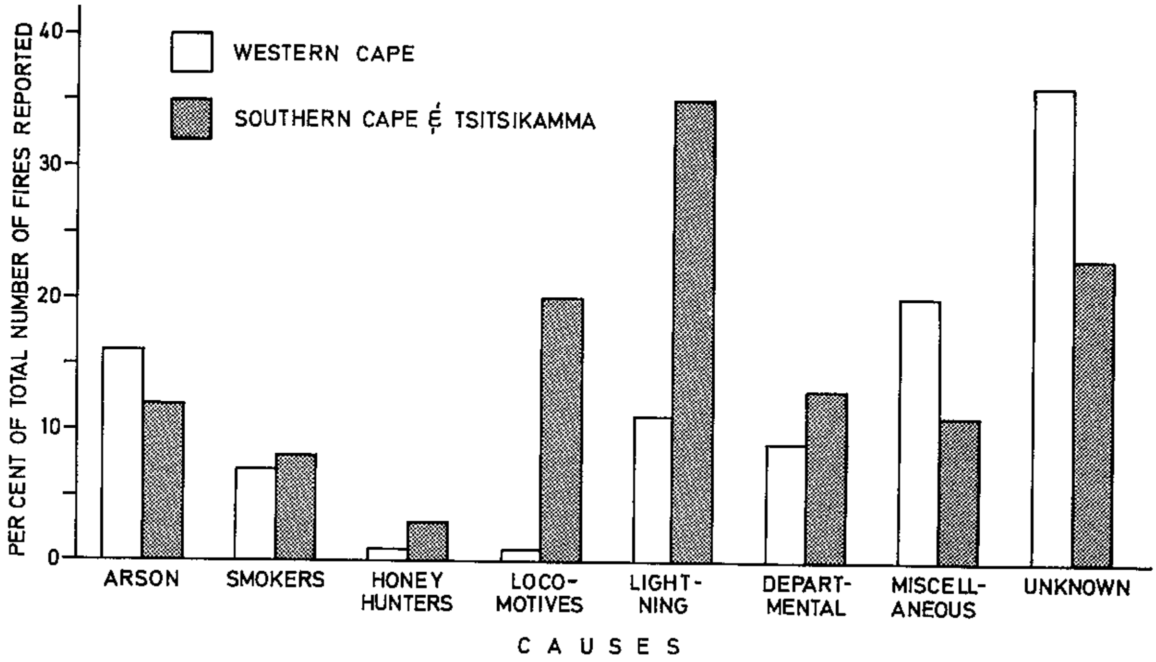

Figure 1. Causes of fires on State Forests in the Fynbos Biome between 1966/67 and 1975/76. Open bars represent fires in the western Cape (294 in total), and shaded bars, fires in the southern Cape and Tsitsikamma (257 in total) Forest Regions. (Data courtesy of P J le Roux, Department of Forestry).

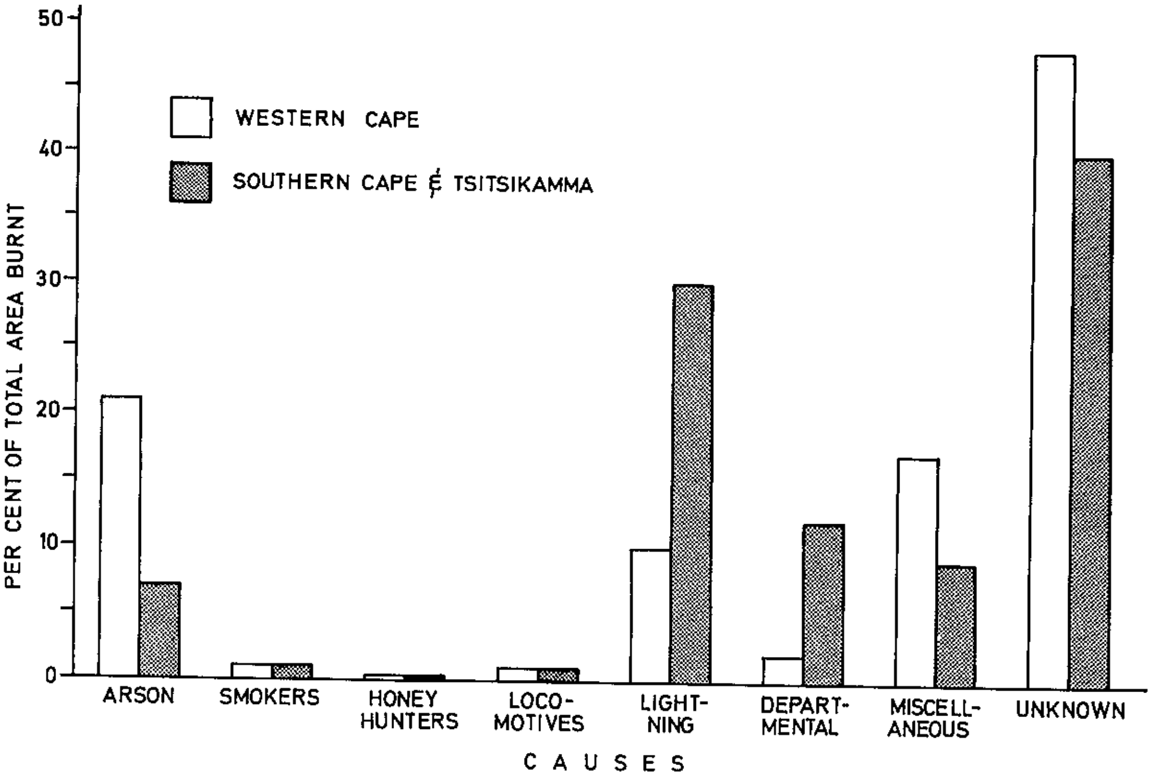

Figure 2. Classification of total area of unafforested State Forest land burnt between 1966/67 and 1975/76 by cause of fire (total area reported is 1 473 km^2). (Data courtesy of P J le Roux, Department of Forestry).

Most fires in areas close to population centres (as in the case of the Cape Peninsula) are presently caused by human activity. On the other hand natural causes of fire are important in remote areas (Kruger in press a), no doubt because natural fires in these areas are preempted less by those caused by people. The Cedarberg is subject to a relatively intensive fire protection system, and is visited by only about 10 000 to 15 000 people annually. This is very likely part of the reason why fires due to human agency are less common and natural fires more common than for example in the Peninsula. Horne (pers comm) reports the same pattern in the Groot-Swartberge.

It is difficult to determine the cause of a given fire. Nevertheless, there are documented eye-witness accounts of fires of natural origin (Wicht 1945). Fires due to lightning strikes are common throughout the fynbos zone, in spite of the relatively low frequency of lightning storms (about five thunderstorms are reported annually at a typical Cape weather station). Although lightning is about ten times more frequent in the areas prone to thunderstorm activity than in the Western Cape (Kröninger 1978), the flash density is nevertheless adequate to explain the relatively high incidence of lightning fires reported in forestry areas (Table 1).

An annual flash density of 1,0 km^{-2} is equivalent to a record of 1 300 ground strikes within the 20 km range of a flash counter. The annual mean at Citrusdal, for example, is equivalent to about 400 strikes per year, which seems more than sufficient to cause a fire within the 1 300 km^2 area every few years.

Falling and rolling rocks arising from natural scarp retreat, earth tremors (which according to Theron (1974) occurred in the southern Cape about 53 times over the past 50 years), and through the activities of baboons, cause fires under suitable conditions of weather and fuel.

There is some indication of a gradient of increasing frequency of natural fires as one proceeds from the coast inland, no doubt due in large measure to increasing frequency of unstable air masses. This would seem worthy of study.

Table 1. Lightning flash densities for selected stations in or on the boundaries of the Fynbos Biome, 1975 to 1978 (from Kröninger 1978).

Station	Location		Flash density
	S Lat	E Long	km^{-2} yr^{-1}
Calvinia	31°28'	19°46'	1,35
Citrusdal	32°35'	19°02'	0,35
De Doorns	33°29'	19°41'	0,33
Hermanus	34°25'	19°14'	0,16
Napier	34°32'	19°54'	0,49
Swellendam	34°02'	20°27'	0,32
Oudtshoorn	33°35'	22°21'	1,53
George	33°58'	22°28'	0,97
Suurberg	33°15'	25°34'	1,31
Grahamstown	33°18'	26°32'	1,47

FREQUENCY OF FIRES

Fire frequency is usually expressed as the frequency per annum at which fires are ignited within a circumscribed area, such as the Cape Peninsula or the Cedarberg. From the biological point of view the burning rotation has more meaning. This is the average time between burns on a given area, i e a return period. The probability that the area will burn is the inverse of the return period. Thus, in a certain mountain range the vegetation on any given site may burn out once in 20 years on average. The probability of fire is therefore 0,05 yr^{-1}.

No rigorous analysis of fire frequency is available for fynbos, but some indication of low fire frequencies can be obtained from records for areas protected against fire. Thus Swartboschkloof, in the Jonkershoek State Forest, burnt out entirely in 1927, 1942 and 1958 (Van der Merwe 1966) and partly in 1973 (Department of Forestry records). Jakkalsrivier, in the Lebanon State Forest burnt in 1947 and 1958, and partly in 1966 and 1967. The Cedarberg State Forest has experienced major fire years in 1929, 1959, 1975 and 1979, in which more than 50 km^2 were burnt.

Fire has been excluded for more than 30 years from only relatively small areas, and then usually by means of intensive firebreaks.

An analysis of fires recorded in the Cedarberg in the interval 1957 to 1975 (from the map in Andrag 1977) indicates an actual burning rotation of between 10 and about 25 years. About 50% of the total area burnt in 1957 to 1959, 11% during 1960 to 1969, and 30% during 1970 to 1975 while about 17% escaped fire during this period. Roughly 30% of the total area burnt twice or more. Almost all burns were wildfires. Contrasting data are available for the Kouga and Baviaanskloof areas, where much of the veld is either transitional fynbos of low productivity (personal observation) and hence less frequently inflammable than typical fynbos, or of a non-inflammable type such as Valley Bushveld, and where in both cases fire protection has been practised since 1959. Management compartments on State Forest in this area have recently been surveyed (Department of Forestry records). Approximately 28% of the total area was judged to be less than five years old, 10% 5 - 10 years, 1,5% 10 - 15 years, 10% 15 - 20 years, and 51% greater than 20 years. Of this oldest category, 0,7% of the total area was classified as 38 years old and the rest between 20 and 38 years old. Data for the southern portion of the Groot-Swartberg indicate a "natural" burning rotation of about 40 years, though the actual rotation observed was 18 years (I P Horne pers comm).

All the cases quoted above are ones where management has been directed at eliminating fires by excluding those from outside by means of perimeter firebreaks, by preventing the spread of those arising inside by means of internal breaks and by extinguishing those that do occur as rapidly as possible. The frequency of fires in these cases can be taken as a lower limit for fynbos ecosystems under present conditions. This is probably lower than the limit under past, pre-settlement conditions, when fires would have spread much more readily in the absence of man-made barriers.

Inherent productivity in fynbos allows sufficient fuel for spreading fires to accumulate only by about the fourth year after the previous fire (Kruger 1977b), but most fynbos vegetation must be somewhat older to burn readily. Therefore it seems that, under a natural fire regime, frequency would have ranged between about once in six to once in 40 years, varying more or less at random between these limits (Kruger 1977a).

FIRE SEASON

The great majority of fynbos communities include a large component of grasses, restios and ericoid shrubs when mature. This component usually amounts to not less than about 6,0 tonnes ha^{-1} (Kruger 1977b). Some communities include up to 10 tonnes ha^{-1} of highly inflammable fine fuel in the form of low resinous shrubs such as Stoebe plumosa (Kruger in press a). The moisture content of this fuel component rapidly follows that of ambient air and will therefore burn in warm sunny conditions, whatever the season. It is not surprising therefore that wildfires are reported in all seasons in any fynbos area (Figures 3 and 4).

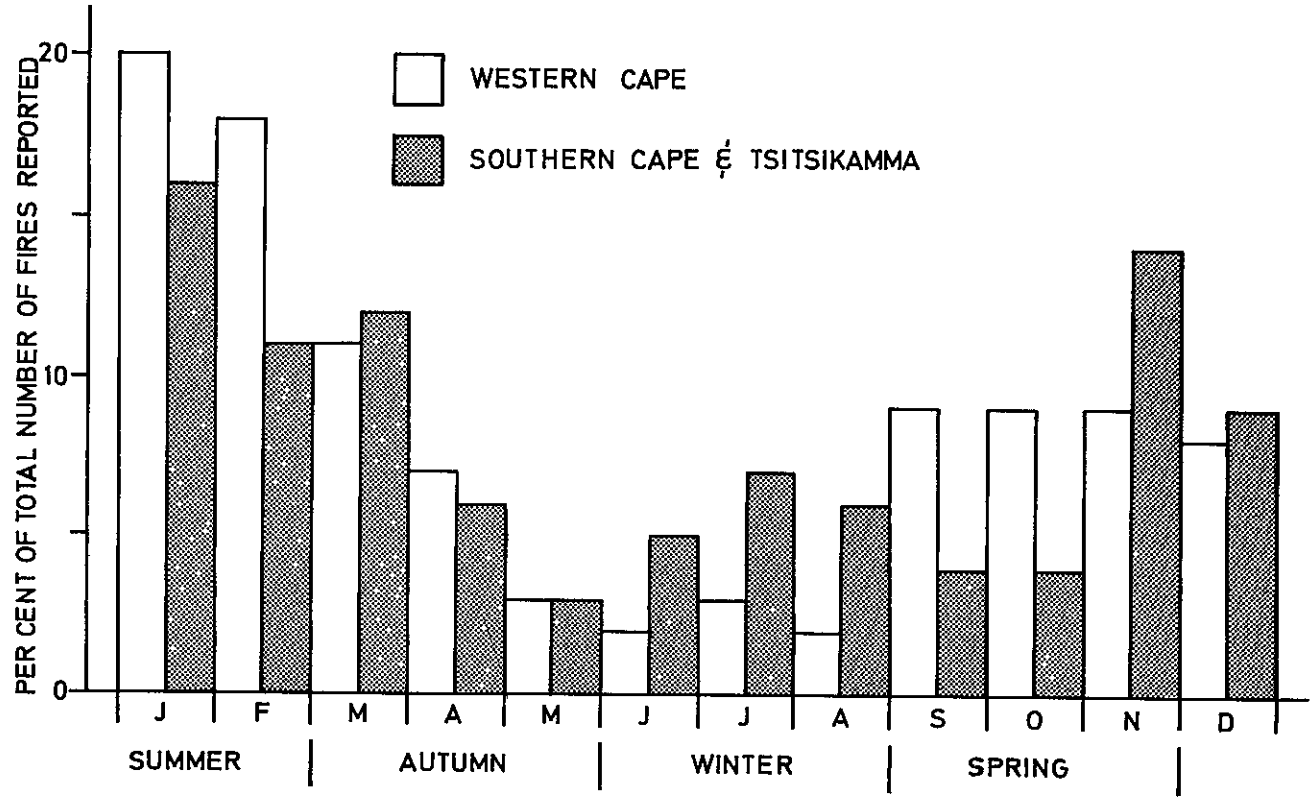

Figure 3. Seasonal incidence of fires on State Forest land in the Fynbos Biome, during 1966/67 to 1975/76. Open bars represent fires in the western Cape and shaded bars those in the southern Cape and Tsitsikamma Forest Regions. (Data courtesy of P J le Roux, Department of Forestry).

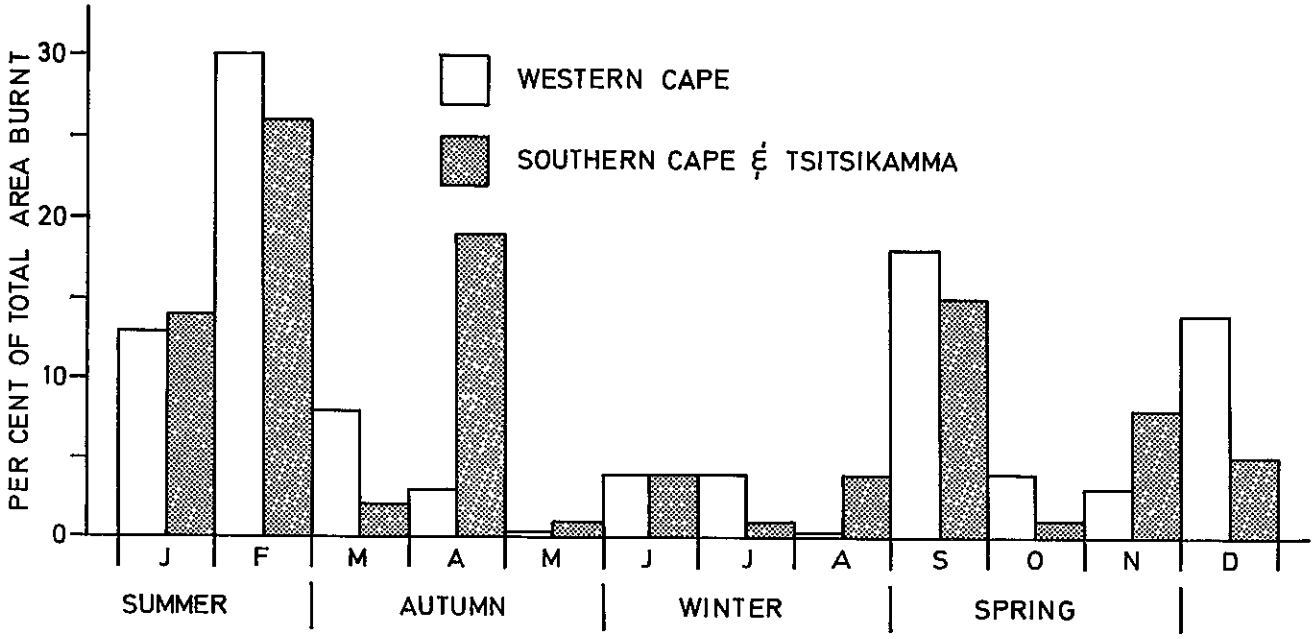

Figure 4. Seasonal distribution of the area burnt on unafforested State Forest land in the Fynbos Biome, between 1966/67 and 1975/76 (total area reported is 1 473 km^2). (Data courtesy of P J le Roux, Department of Forestry).

Nevertheless, most fynbos fires occur in summer when they burn the largest areas, except that fires are frequent in the winter in the southern Cape when they often burn large areas (Le Roux 1969).

The seasonal incidence of lightning would crudely indicate the possible seasonality of natural fires in fynbos. Of 18 lightning counter stations in the Fynbos Biome, with relatively complete records for 1978, six had maximum flash density records in the summer of 1978, seven in the autumn, three in winter, and two in spring (Kröninger pers comm). Department of Forestry reports for the ten years 1966/67 to 1975/76 show that lightning fires occurred in all months but June and July and that most large lightning fires tend to occur in summer (see Table 2.2 in Kruger in press a). Horne (pers comm) reports that 75% of fires, whether natural or otherwise, in the Groot-Swartberg occurred between October and March, inclusive.

FIRE INTENSITY AND BEHAVIOUR

There are few studies of fire intensity and behaviour in fynbos. Table 2 contains estimates of energy release rates from typical fynbos fires.

Table 2. Estimated fire intensities for a range of fuel loads, under a range of normal fire weather conditions1/ (Bands 1977)

	Minimum	Intermediate	Maximum
Available fuel (kg m^{-2})	0,30	0,70	1,00
Rate of spread (m sec-1)	0,07	0,28	1,11
Byram index (kW m^{-1})	360	3300	18900

1/ Fuel estimates based on data in Kruger (1977b) and rate of spread based on personal observation.

Fynbos fires are not exceptionally intense, and have rates of advance rather slower than for example those in humid grassland with similar amounts of available fuel. Nevertheless, because vegetation is rather tall, and the available fuel is well dispersed in a layer up to 1,0 to 1,5 m deep, flames tend to be rather high (2,0 to 5,0 m) and flame fronts deep (1,0 to 6,0 m). These fires are consequently difficult to control, especially in the prevailing rugged terrain.

Behaviour characteristic of very intense fires, such as powerful fire-whirls and long-range spotting, is not the rule in most fynbos fires. However, under severe weather and fuel conditions the picture changes, and extreme rates of advance (over 4 km hr^{-1}) with moderate spotting (fires carried 200 m or more) are usually reported under hot windy conditions. The large fynbos fires (such as those listed in Table 3) almost all occur under relatively rare, severe weather conditions. Thus, the large Cedarberg fires of 1975 and 1979 occurred in heat-wave conditions, when midday air temperatures exceeded 35 to 40°C, relative humidity fell to 10 to 20% and turbulent, erratic winds prevailed. The fire of May 1975 in the Kouga spread furthest under berg wind conditions, when temperatures exceeded 30°C, in spite of typical winter weather before and after the fire.

Table 3. Some large fynbos fires (data from Bands (1977) and Department of Forestry records).

Locality of fire	Area (km^2)	No of ignition points	Date	Duration (days)	Predomanant age of veld (yrs)
Hottentots-Holland Mtns	112,0	2	Dec 1942	18	15-20
Hottentots-Holland Mtns	171,3	2	Jan 1958	16	approx 16
Du Toits Kloof Mtns[1]	180,0	5	Feb/March 1971	17	10-20
Krakadouwpoort, Cedarberg State Forest[1]	27,0	approx 5	Dec 1972	4	approx 38
Krakadouw-Groot Koupoort, Cedarberg State Forest	59,5	1	Feb 1975	5	approx 40
Kouga Mountains, Baviaans-kloof State Forest	187,0	1	May 1975	10	20-35
Sneeuberg, Cedarberg S F	135,0	1	Dec 1975	6	15
Heksberg, Kouebokkeveld Mountains	300,0	1	Feb 1976	10	30-35
Langeberg Mountains, Garcia State Forest[1]	26,8	9	March 1977	4	15-25
Middelberg-Boskloof, Cedarberg State Forest	107,0	1	January 1979	8	approx 15

[1] causes include lightning.

Wicht and De Villiers (1963) and Le Roux (1969) have emphasized the importance of weather, rather than season, on the occurrence of damaging fynbos fires. Fires may occur at any time when conditions are warm and dry but here, as elsewhere (McCutchan (1977) gives examples from California), most do not spread to any great extent. The weather conditions that favour the large fire occur rather irregularly, perhaps only once or a few times per year at any one place, and not necessarily in mid-summer. In the George - Knysna area, some of the largest and most destructive fires have occurred in winter (Le Roux 1969).

SYNOPSIS

The picture which emerges from the rather scanty data available is one of a rather variable modern fire regime. The degree and nature of variability in frequency and season are depicted hypothetically in Figures 5 and 6. These hypotheses are probably too simple. For example, the frequency of spring and autumn fires in the southern Cape may be higher than suggested in Figure 5, but they do reflect the stochastic nature of the available data and the essential trends discernible. It is difficult to account for other elements of variability without more comprehensive data. Major conflagrations appear to be relatively unpredictable in respect of season, for example, but there certainly is a tendency for these to occur in the summer and autumn in the west, and in winter in the east.

Fire intensity is very poorly documented but since intense fires are usually large it is likely that fynbos would be subject to more high-intensity and fewer low-intensity burns.

Understanding fynbos ecology would be greatly assisted if the fire regimes under which the biota evolved were known. However, past fire regimes cannot be reconstructed in the absence of data, for example from well-preserved fossil carbon in annually laminated Quaternary sediments, and from long-lived trees with regular annual rings, such as have been used elsewhere e g Swain (1973), and other papers in Wright and Heinselman (1973).

Any attempt to do so without data from such sources is purely a speculative exercise. Nevertheless, it seems that without major vegetation change it is unlikely that past fire regimes would have differed markedly from the modern one,

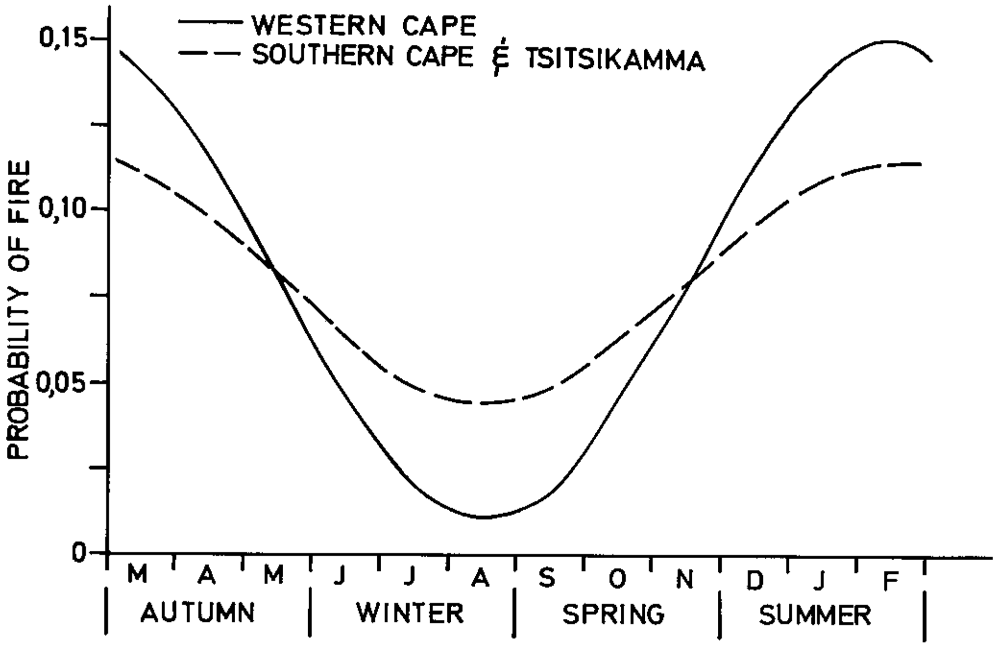

Figure 5. Hypothetical seasonal fire frequencies for the Fynbos Biome. Solid line represents a "western" fire regime, and broken line, an "eastern" fire regime.

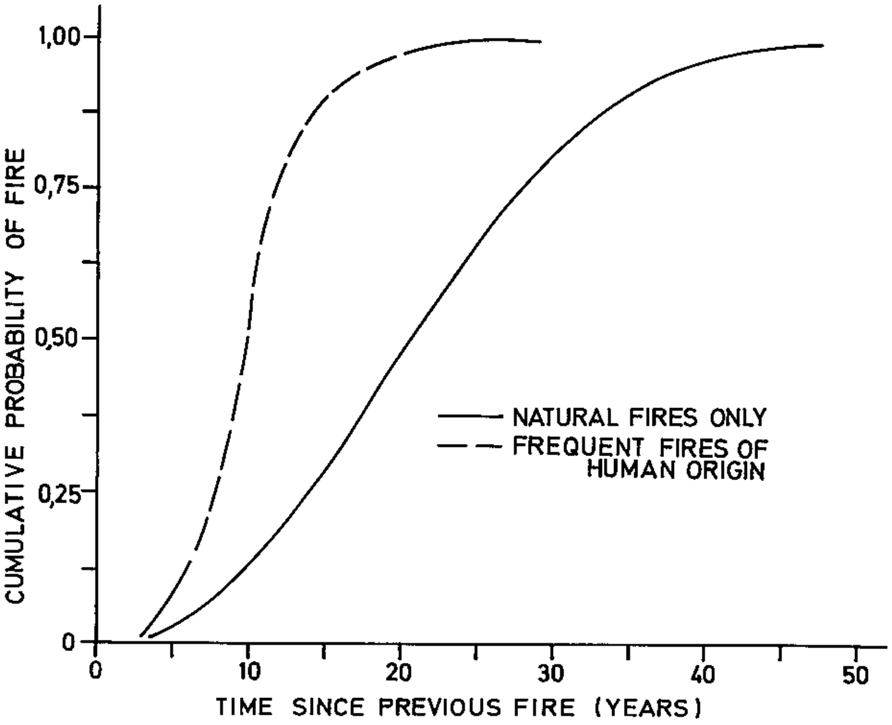

Figure 6. Hypothetical fire frequencies, expressed as cumulative probabilities of occurrence over any given area, as a function of time since previous fire (the burning rotation). Solid line represents a probability function for an area where fires of human origin are at a minimum, and broken line that for an area with many fires of human origin.

in cases where human influence is not strong, and would have approximated those presented in Figures 5 and 6, especially in their stochastic nature. This would also seem to accord with the nature of the fynbos flora where, for example, in any community species are typically divergent in their growth forms, demographics and seasonalities, and thus in their response to fire (see Kruger 1977a, in press a, in press b). It seems unlikely that such diversity could have evolved in a highly regular fire regime.

REFERENCES

Alexander J E 1838. An expedition of discovery into the interior of Africa. Henry Colburn, London. 2 Vols.

Andrag R H 1977. Studies in die Sederberge oor (i) die status van die Clanwilliam seder *Widdringtonia cedarbergensis* Marsh (ii) buitelugontspanning. MSc thesis, Univ of Stellenbosch. 141 pp.

Bands D P 1977. Prescribed burning in Cape fynbos. Proceedings of the Symposium on the Environmental Consequences of Fire and Fuel Management in Mediterranean Ecosystems. USDA Forest Service. General Technical Report WO-3. pp 245-256.

Botha C G 1924. Note on early veld burning in the Cape Colony. South African Journal of Science 21, 351-352.

Brown J C 1875. Hydrology of South Africa. Henry King and Co, London. 260 pp.

Brown J C 1887. Management of the Crown Forests at the Cape of Good Hope under the old regime and under the new. Oliver and Boyd, Edinburgh; Simpkin, Marshall and Co, London. 352 pp.

Burrows E H 1952. Overberg outspan. Maskew Millar, Cape Town.

Kröninger H 1978. Newsletter, National Lightning Recording Scheme, No 2, November 1978. CSIR, Pretoria, National Electrical Engineering Research Institute, Special Report ELEK 161, pp 1-18.

Kruger F J 1977a. Ecology of Cape fynbos in relation to fire. Proceedings of the Symposium on the Environmental Consequences of Fire and Fuel Management in Mediterranean Ecosystems. USDA Forest Service. General Technical Report WO-3. pp 230-244.

Kruger F J 1977b. A preliminary account of aerial plant biomass in fynbos communities of the mediterranean-type climate zone of the Cape Province. Bothalia 12, 301-307.

Kruger F J (in press a). South African heathlands. In: Ecosystems of the world. Vol 9. Heathlands and related shrublands. R L Specht (ed). Elsevier, Amsterdam.

Kruger F J (in press b). Seasonal growth and flowering rhythms: South African heathlands. In: Ecosystems of the World. Vol 9. Heathlands and related shrublands. R L Specht (ed). Elsevier, Amsterdam.

Le Roux P J 1969. Brandbestryding in Suid-Kaapland met spesiale verwysing na chemiese metodes van beheer. MSc thesis, Univ of Stellenbosch. 157 pp.

McCutchan M H 1977. Climatic features as a fire determinant. Proceedings of the Symposium on the Environmental Consequences of Fire and Fuel Management in Mediterranean Ecosystems. USDA Forest Service. General Technical Report WO-3. pp 1-11.

Pappe L 1855. Silva Capensis. Ward & Co, London.

Swain A M 1973. A history of fire and vegetation in northeastern Minnesota as recorded in lake sediments. Quarternary Research 3, 383-396.

Taylor H C 1969. Pesplante en natuurbewaring. Forestry in South Africa 10, 41-46.

Theron J N 1974. The seismic history of the southwestern Cape Province. In: The earthquake of 29 September 1969 in the Southwestern Cape Province, South Africa. W L Van Wyk and L E Kent (eds). Geological Survey, Dept of Mines, Pretoria Seismologic Series 4, pp 12-18.

Van der Merwe P 1966. Die flora van Swartboschkloof, Stellenbosch en die herstel van die soorte na 'n brand. Annale Universiteit van Stellenbosch 41 Serie A(14), 691-736.

Wicht C L 1945. Report of the committee on the preservation of the vegetation of the southwestern Cape. Special Publication of the Royal Society of South Africa, Cape Town.

Wicht C L and Y R de Villiers 1963. Weerstoestande en brandgevaar by Hermanus. Journal of Geography 2, 25-36.

Wicht C L and F J Kruger 1973. Die ontwikkeling van bergveldbestuur in Suid-Afrika. South African Forestry Journal 86, 1-17.

Wright H E and M L Heinselman (eds) 1973. The ecological role of fire in natural conifer forests of western and northern America. Quaternary Research 3, 317-513.

PALAEOECOLOGY

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The study of the palaeoecology of the Fynbos Biome is the study of the history of the southern margin of the African continent as reflected in the geological deposits and the fossils they contain. In terms of biological interest, the present day floras and faunas are the product of evolution and dispersal through time in this region corresponding physiographically with the Cape Folded Mountains and their attendant coast. Rocks of the Cape Supergroup are dominant although there are limited inliers evidencing an earlier period in the geological history when geological sediments, approximately conformable to the continental margin, were accumulated, deformed as the Malmesbury-Cango fold belt, and in a late phase of deformation were intruded by granite plutons. The latter geological event is radiometrically dated to 553±8 My (million years) (Bishopp and Van Eeden 1971, Table 1). It was on the planed surface of these earlier rocks that the predominantly shallow marine sediments of the Cape Supergroup were laid down in a basin depository (Rust 1973) in late Silurian and Devonian times (400 My). In turn these strata were folded and given positive relief during the Cape-Karoo orogeny by folding along lines mirroring the structural trends of earlier times. The Cape Folded Belt then bordered the inland Karoo cratonic basin and the strata accumulating in this basin represent a record of the reptilian faunas and floras (such as the Glossopteris flora) of a very different stage in biological history. However, some authorities, notably Melville and Plumstead (for discussion see Hughes 1976 p 194), have argued that, in details of the morphology of the fructifications and leaf venation of Glossopteris, the equivalent angiosperm structures are anticipated and that there is a continuity traceable to the present.

The continental margin, outlined by prior folding, was formed at the end of the Jurassic (140 My) by crustal rifting along the western side and by shearing along a zone corresponding to the outer edge of the Agulhas Bank (Siesser, Scrutton and Simpson 1974). This event marks the separation of the African plate from the South American plate (Sclater, Hellinger and Tapscott 1977). Penecontemporaneous and possibly related normal faulting, with significant downthrows to the south but little lateral movement along the southern flanks of

Table 1. Time shown on a log scale with geological periods and stages in the evolution of the Fynbos Biome

thousands of years	10	CENOZOIC (= Tertiary + Pleistocene + Holocene)	HOLOCENE	*Present-day communities - present-day climates.* *End-Pleistocene extinction of five large mammal taxa.*
	20 30		PLEISTOCENE (Last Glacial)	*Maximum cold of Late Pleistocene; sea levels -124m lower, exposed coastal shelf served as migration route for plants and animals.*
				Pleistocene climates cooler overall than the present; coastal forelands and intermontane valleys had more open vegetation communities with grasses an important component; mammal fauna dominated by Alcelaphine antelope.
	200 300			*Mid-Pleistocene fauna more diverse than in the present, but dominated by species ancestral to modern African taxa.*
				Pleistocene oscillations in climate requiring dynamic adjustments in vegetation communities contributing to a high index of diversity.
millions of years	2			*Inception of current climatic systems in the Plio-Pleistocene.*
	3		PLIOCENE	*Elevation of the mountains continuing since the Miocene.* *Ancestral fynbos communities indicated in the pollen record.* *Archaic mammal fauna - all species and many genera extinct.*
	10 20		MIOCENE	*Mio-Pliocene Bredasdorp and Alexandria beds deposited on coastal platform forming new substrates for evolution of limestone endemics.* *Alternation between dominance by tropical palm and temperate vegetation recorded in pollens from boreholes in SW Cape.*
	30		OLIGOCENE	*Knysna wood beds; Proteaceae, Restionaceae and forest taxa.*
			EOCENE	*Planation of the Cape coastal platform.*
			PALEOCENE	*Austral connections severed.*
	100	MESOZOIC	CRETACEOUS	*Local lower Cretaceous basins; pre-Angiosperm flora.*
			JURASSIC	*Crustal rifting and opening of the South Atlantic initiated.*
	200		PERMO-TRIAS	*Deposition in the Karoo cratonic basin - Glossopteris flora.* *Cape-Karoo orogeny - initiation of the fold belt system.*
	300	PALEOZOIC	DEVONIAN SILURIAN	*Cape Supergroup sedimentary cycle.*
	1000	PRE-CAMBRIAN		*Folding and intrusion of granite plutons.* *Malmesbury-Cango sedimentary cycle.*

the anticlinal folds of the Cape mountains, (the Worcester fault is an example), had an effect on relief and created minor basins of lower Cretaceous fluviatile, estuarine and transgressive marine sedimentation (Bishopp and Van Eeden 1971). One example, the Uitenhage basin, preserves a late Mesozoic reptile fauna and a pre-angiosperm flora represented by macroscopic plant remains and pollens. Palynologically the flora belongs to a southern Gondwana province and is dominated by bisaccates of Podocarpaceae, although other gymnosperms and diverse pteridophytes are represented (Brenner 1976). This could be seen as an early austral forest, represented again in the succeeding early Cenozoic (65 - 23 My) by occurrences of fossil wood and leaves in the Fort Grey and Knysna wood bed occurrences (Levyns 1964) and in the present day by the temperate evergreen Knysna forest. The Cenozoic (65 - 0 My) geological history of the continental margin is better documented in the offshore than in the shore deposits, but outward flexuring of the continental margins and faulting resulted in a series of marine transgressions and regressions that are reflected in deposits now above sea-level. These events and their timing are important because along the coast, for example, substrates were formed to which the limestone endemics of the Coastal Fynbos are adapted. Again, the flexuring was responsible for raising the altitudinal range of the mountains with the creation of the range of niches occupied by the present flora and fauna. Studies in marine geology along the Cape coast can contribute to the understanding of the palaeoecology of the biome because of the incomplete nature of the record of geological events preserved on the land.

The Cape region has been described as preserving possibly the most bizarre relict biota in the world to-day (Livingstone 1975). This has to do with the retention into the present of archaic austral elements in the flora. The major factor involved is that Africa was in effect an island continent from the late Cretaceous through the early Cenozoic. Some modern thinking at least would accord with the statement by Van Zinderen Bakker (1976) that the nuclei of the biota of southern Africa are of Gondwana origin, and that contact with the flora and fauna of the Northern Hemisphere has been limited. Indeed, it can be suggested that faunal and floral interchange with Eurasia was significant only from the earliest Miocene (23 My). As has been pointed out by Kurtén (1973), in the early Cenozoic the faunas of Africa show the evolution of local endemic orders and families; the same trends can be suggested in the floras. In later times, South Africa and the Cape were remote from the zone of optimal interchange and were cut off from northern temperate floras by a barrier of tropical forest. Far from being a constant environment through time, the relict biota at the Cape has survived in a zone sensitive to change and its history is a subject of some interest.

There are a number of families in the Cape flora, notably the Proteaceae and Restionaceae, which have been noted by Levyns (1964) as examples of southern disjuncts, that is with representatives in the floras of other southern continents. A survey of the contemporary temperate biotas of the southern continents, however, shows that of South Africa to be the most distantly related. It is still a matter of debate, in spite of a growing corpus of information on the history of the continents and ocean floors, as to when the links between Africa and the other southern continents were severed. Accepting a mid- to late-Cretaceous dating for the diversification of the angiosperms, this is subsequent to the Jurassic or earlier breakaway of Madagascar on the east and the end-Jurassic (130 My) initial opening of the Atlantic through rifting along the west coast of Africa. Schuster (1976) has suggested the presence of archipelagic connections, admittedly diffuse, between eastern Africa via the Mascarene ridge (Seychelles) and Madagascar and the other southern continents until as late as 75 My. More direct interchange between Africa and South America was possible via the Falkland Island plateau, via the Walvis/Rio Grande ridge and in the area of the bulge of Africa in the Cretaceous (Sclater et al 1977) until perhaps as recently as 100 My. The latter figure is the most acceptable estimate of the period of isolation of the austral element in the flora.

In the Cenozoic the oceanic circulation patterns and the major climatic and ecological zones in Africa were established in a form tending towards that of the present. The continent had achieved its near-modern outline by the beginning of the Cretaceous but latitudinal northward movement of the African plate through some 10^{o} to a conjunction with the Eurasian plate was only completed by the mid-Cenozoic. This movement had the effect of displacing climatic zones southward and, for example, a reconstruction of the climate at the beginning of the Cenozoic (Robinson 1973) places the Cape in a zone of cool wet climate and the equatorial zone then traversed north Africa in the present position of the southern Sahara. Ocean circulations were affected by the conjunction of the continents as well as by the stage-by-stage opening of the Atlantic. By the early Oligocene (36 My) the South Atlantic was open to Antarctic bottom waters (Sclater et al 1977) and the climate of the western coast of southern Africa came increasingly under the influence of a cold off-shore current. Most authorities are agreed, however, that the present hyper-aridity of the Namib coast did not develop until after the end of the Miocene (6 My) when the Antarctic ice sheets reached their present proportions (Axelrod and Raven 1978, Coetzee 1978). A similar late-Tertiary dating for the inception of winter rainfall climate in the south-western Cape as inferred by Levyns (1964) can be supported.

A recent review of the vegetation history of Africa since the Cretaceous (Axelrod and Raven 1978) points out that with increased dryness through the Cenozoic, the main trend has been the expansion of savanna at the expense of forest and the development of areas of sclerophyllous vegetation and thorn scrub at drier sites, culminating, as noted above, in the appearance of regional semi-desert and desert areas at the end of the Cenozoic. In this review, the implications for the origins of the fynbos lie in the suggestion of an early development of an ancestral sclerophyllous vegetation adapted to seasonal drought in the western part of southern Africa, to the north of the present distribution of fynbos. This is in line with Levyns' (1964) postulate that, apart from the smaller ancestral component in the Cape flora, the majority of taxa have had a more northerly origin. An ancestral vegetation of this type could have served as a source for the recruitment of taxa to the fynbos as it developed under Plio-Pleistocene winter rainfall conditions. That winter rainfall conditions are relatively recent and that recruitment of taxa was from adjoining summer rainfall regions is supported by Levyns' (1964) observation that some taxa in the Cape flora retain a growth regime that is not fully adapted to dry summer conditions. In considering the origins of the fynbos vegetation it is important to appreciate that its Tertiary antecedents were floristically more diverse and the associations of taxa were different from those found in modern communities developed in the Pleistocene.

Palynological studies of borehole cores from the south-western Cape (Coetzee 1978) are serving as a test of the reconstructions of the past vegetation distributions and they are providing new insights into the vegetation history of the Fynbos Biome. Records currently available cover the time range from the mid-Cenozoic to the present and confirm the greater diversity of the Tertiary vegetation and the occurrence of significant vegetation changes in the Cenozoic. Coetzee (1978) has inferred alternation between cool, wet forests, indicated by a dominance of Podocarpaceae pollens, and more sub-tropical or tropical vegetation, indicated by a dominance of palm pollens in the period from the Oligocene to the Pliocene. Pollens of more typical fynbos taxa are represented in Pliocene and Pleistocene strata. Possibly the best dated Pliocene polleniferous occurrence is associated with the Quartzose Sand Member of the Varswater Formation at Langebaanweg (Hendey and Deacon 1977). An age of some 5 My, or earliest Pliocene, can be assigned to this deposit on the basis of faunal correlations with radiometrically dated faunal occurrences in East Africa. The fauna is more diverse than any historically known from the south-western Cape and vegetation communities of that time are unlikely to have any modern analogue; however, the main polleniferous horizon shows a relative importance of Ericaceae and Compositae. This could indicate the appearance of associations of fynbos which are more characteristic in the south-western Cape, but it is not possible to interpret the evidence directly in terms of specific communities.

Coetzee's study gives a good indication of the degree to which the flora of the south-western Cape was impoverished through extinctions of both tropical and austral elements in the later Cenozoic. Hitherto there has not been a basis for comparison with well studied Tertiary floras of the other southern continents and indeed the Tertiary flora of South Africa has been poorly known. The pattern of alternation between temperate and sub-tropical vegetation is explicable in terms of the model of the vegetation history afforded by the reconstruction of Axelrod and Raven (1978), if it is assumed that vegetation zones were displaced southwards and eastwards along the southern continental margin under conditions of increasing aridity on the south-west coast through the strengthening of the Benguela current, cold water upwellings and the stabilization of the South Atlantic anticyclone system (Van Zinderen Bakker 1975, Coetzee 1978). This follows Levyns' (1964) postulate of fynbos displacing the temperate forest flora in the Cape Folded Mountain region in the late Tertiary. The Knysna forest is clearly a relict with outliers throughout the Cape region and palms, although not of the same taxa as represented in the Tertiary, have a present distribution as far south as the Bathurst coast on the eastern margins of the Cape Folded Belt. The ecotone between temperate and sub-tropical vegetation on the Coastal Foreland is thus eastwards of the Mio-Pliocene position. The scale of vegetation changes in the Tertiary, shown by the palynological study, highlights the problem of interpreting disjunct distributions and relicts in the flora. Some anomalous distributions that have been suggested as being due to recent human impact on the vegetation, or again to Pleistocene climatic changes, could well prove to be older than expected. A case in point is the reconstructed map of the vegetation in A D 1400 by Acocks (1953) which in itself is a notable compilation. The reconstruction of the former distribution of veld types in the fynbos region indicated on the map, however, suffers from telescoping the time depth of changes that were initiated in the Tertiary and have continued into the present.

Speciation in the Cape flora is clearly a secondary feature in that it has taken place after the associations of taxa in the flora were established. Levyns (1964) has suggested that the seasonal distribution of rainfall, i e winter rainfall conditions, rather than the absolute amount of precipitation, has been a factor in inducing a high rate of speciation. Axelrod and Raven (1978), on the other hand, consider that topographic changes through continental uplift in the mid- and late-Cenozoic may have been a factor in initiating bursts of speciation and Van Zinderen Bakker (1976) and Deacon (1976) have stressed the role of Pleistocene climatic changes. The possibility then is that the factors inducing speciation have been operative throughout the later Cenozoic and that speciation may be a process continuing to-day.

While the Cape flora is known for its richness in species, the distribution of species is not uniform and shows definable foci or centres of concentration (Weimarck 1941). Similar centres occur outside the Fynbos Biome and do not necessarily include taxa typical of the Cape flora. The pattern can be illustrated by reference to the genus Euryops (Compositae) (Nordenstam 1969). The most primitive section, Angustifolia, has a geographical range down the high eastern side of Africa from Arabia to the Cape, but the more advanced sections are restricted in distribution to South Africa. Of a total of 97 species included in the genus, 89 occur in southern Africa. The occurrence of the genus on both sides of the Red Sea rift and on the island of Socotra suggests the primary distribution was established early in the Miocene (20 My) and speciation in South Africa was secondary and more recent. Within South Africa there are few species in the more arid areas and interior plateau and the main concentration is within the Cape Folded Belt and its northern extension to the Orange River, and along the Great

Escarpment including the Drakensberg. On the basis of the phytogeography of Euryops, Nordenstam defines 9 centres, one of which is the south-western Cape or Caledon centre, an important locus for the concentration of species of taxa more typical of the Cape flora. It is possible to hold, as does Nordenstam (1969), that these are centres of evolution or active speciation, or again that they are refugia in broken upland situations. What is noteworthy is the ripple-like decrease in the numbers of species in a given genus found outwards from the core areas or centres. That these centres have been able to maintain their distinctive character suggests that interchange between centres during more recent Pleistocene environmental changes may have been limited.

The origin and speciation of the Cape flora involves consideration of long time periods, but the vegetation communities of the present do not share this same long history. They are the product of dynamic adjustments amongst loose associations of taxa that have changed in response to external stimuli such as climatic oscillations, fire, grazing or browsing by animals and the impact of human activities. Thus while the taxa have been present in the Cape flora for a considerable period of time, the association of specific taxa in the communities that can be delimited to-day is recent. The present-day communities and their distributions are in a strict sense a response to the present Holocene interglacial conditions which developed 10 000 years ago and are thus very recent. However, for a perspective on the development of present day communities, a perspective on the environmental changes of the Pleistocene is necessary.

The Pleistocene was a period when global climates were affected by the alternate expansion and contraction of high-latitude continental ice sheets. Deep-sea core records show glacial events to have a periodicity of some 100 000 years and there have been between seven and eight glaciations in the last 700 000 years. The glacial cycles each represent a long period of reduced mean temperature with shorter interglacial periods of climatic amelioration, lasting about 10 000 years. In the latitude of the Fynbos Biome the expected depression of temperature during a glacial maximum would be of the order of 5°C below that of the present. More precise estimates will become available through oxygen isotope studies of speleotherms and other materials, currently in progress. The mountains of the Cape Folded Belt were not glaciated during the Pleistocene but in the south-western Cape they do show clear evidence of former colder climate in mantles of frost-fractured blocky screes (Goede pers comm). It is more difficult to gain a measure of the scale of precipitation changes or again to infer any pattern in periods of increased or decreased rainfall on present observations, but good palynological and geomorphological evidence does exist for episodes of higher precipitation. It seems that the Pleistocene represents a period of relatively rapid climatic oscillation, the cumulative effects of which can be invoked as a partial explanation of the complexity seen in modern vegetation communities.

The aim of current research is to gain a measure of the changes in the faunal and floral distributions during the most recent glacial-interglacial cycle, that of the Upper Pleistocene/Holocene, covering the last 100 000 years. This time range is the most relevant to the evolution of present-day ecosystems and palaeoecological studies can give a perspective of dynamic changes that cannot be replicated by experiment because of the time scales involved.

The study of palaeontological occurrences and the relatively few palynological observations available (Van Zinderen Bakker 1976), together with the study of macroscopic plant remains (Deacon 1976) show that with relatively minor departures the present floral and faunal distributions were established at the beginning of the Holocene. There is scope to amplify the Holocene record and such studies are in progress. Significant changes in the fauna and, by inference, the vegetation are evident in the terminal Pleistocene. More direct evidence of floral changes is also being accumulated.

In the late Pleistocene, at the maximum of the last glacial, sea levels were lowered by some 120 m and this had the effect of considerably extending the Coastal Foreland southwards. The maximal extension was along that part of the coast bordering the Agulhas bank and this extension made migration of both plants and animals possible along a now submerged section of the coastal plain. The closest modern analogue to the habitat created by eustatic lowering of sea-level is the Bredasdorp coast. The edaphic constraint of clayey substrates suggests that the vegetation was dominated by grasses and this is supported by the dominant alcelaphine and equid fauna from palaeontological occurrences dated between 18 000 and 10 000 years before the present from coastal sites in the southern Cape (Klein 1977).

Inland of the coast in the intermontane valleys there is palynological and palaeontological evidence that the climate of the last glacial maximum was both dry and cold in the southern Cape with some expansion of Karoo vegetation, for example in the foothills of the Swartberg. In the latter habitats in the terminal Pleistocene, after the glacial maximum, the large mammal fauna is again dominated by grazers, in contrast to the browsers dominating the Holocene and present day large mammal fauna. This suggests that in the late Pleistocene the vegetation of the intermontane valleys in the Cape Folded Belt was open woodland or grassland rather than the shrubland vegetation of the present. The study of dated series of charcoal samples from stratified deposits in the foothill zone of the Swartberg shows significant changes in the woody component in the vegetation between the terminal Pleistocene and the Holocene and again in the late Holocene. In the cold Upper Pleistocene, reduced temperatures, coupled to the increased incidence of ground frost in the valley bottoms and to snowfalls persisting longer on the mountain ranges, can be seen as a factor in isolating communities, in particular Mountain Fynbos communities, and restricting the geographical range of certain taxa. Many more observations will be necessary to gain a more comprehensive picture of the palaeoecology of the Fynbos Biome even in the most recent past.

Although the scale of palaeoecological investigations in the fynbos has been very limited to date, there is obvious scope for extending these in several directions. Palynology has increasingly come into its own as a technique for the study of the history of floras. There is scope for launching a full-scale study of known fossil occurrences like the Knysna wood beds, re-sampling of earlier Cenozoic sites reported in the literature, and investigating new occurrences being discovered by mining operations, building and drilling. For the late Pleistocene and Holocene, more occurrences are known and there is potential for relatively detailed reconstructions of past environments, which will have relevance to present day problems of conservation and management.

REFERENCES

Acocks J P H 1953. Veld types of South Africa. Memoirs of the Botanical Survey of South Africa 28, 1-192.

Axelrod D I and P H Raven 1978. Late Cretaceous and Tertiary vegetation history of Africa. Biogeography and ecology of Southern Africa. M J A Werger (ed). W Junk, The Hague. pp 77-130.

Bishopp D W and O R van Eeden 1971. Explanatory text for the tectonic map of Africa: areas co-ordinated by the southern group. Tectonics of Africa. UNESCO, Paris.

Brenner N 1976. Middle Cretaceous floral provinces and early migrations of angiosperms. Origin and early evolution of angiosperms. C B Beck (ed). Columbia University Press, New York. pp 23-47.

Coetzee J A 1978. Climatic and biological changes in south-western Africa during the late Cenozoic. Palaeoecology of Africa 10, 13-29.

Deacon H J 1976. Where hunters gathered. South African Archaeological Society, Claremont.

Hendey Q B and H J Deacon 1977. Studies in palaeontology and archaeology in the Saldanha region. Transactions of the Royal Society of South Africa 42, 371-81.

Hughes N F 1976. Palaeobiology of angiosperm origins. Cambridge University Press, Cambridge.

Klein R G 1977. The ecology of early man in southern Africa. Science 197, 115-26.

Kurtén B 1973. Early Tertiary land mammals. Atlas of Palaeobiogeography. A Hallam (ed). Elsevier, Amsterdam.

Levyns M R 1964. Migrations and origin of the Cape flora. Transactions of the Royal Society of South Africa 37, 85-107.

Livingstone D A 1975. Late Quaternary climatic change in Africa. Annual Review of Ecology and Systematics 6, 249-80.

Nordenstam B 1969. Phytogeography of the genus Euryops (Compositae). Opera Botanica 23, 1-77.

Robinson P L 1973. Palaeoclimatology and continental drift. Implications of continental drift to the earth sciences D H Tarling and S K Runcorn (eds). Academic Press, London. 1, 451-76.

Rust I C 1973. The evolution of the Palaeozoic Cape basin, southern margin of Africa. The ocean basins and margins. A E M Nairn and F G Stehli (eds). Plenum Press, New York. pp 247-76.

Schuster R M 1976. Plate tectonics and its bearing on the geographical origin and dispersal of angiosperms. Origin and early evolution of angiosperms. C B Beck (ed). Columbia University Press, New York.

Sclater J C, S Hellinger and C Tapscott 1977. The palaeobathymetry of the Atlantic ocean from the Jurassic to the present. Journal of Geology 85, 509-52.

Siesser W G, R A Scrutton and E S W Simpson 1974. Atlantic and Indian ocean margins of southern Africa. The geology of continental margins. C A Burk and C L Drake (eds). Springer-Verlag, New York.

Van Zinderen Bakker E M 1975. The origin and palaeoenvironment of the Namib desert biome. Journal of Biogeography 2, 65-73.

Van Zinderen Bakker E M 1976. The evolution of late Quaternary palaeoclimates of southern Africa. Palaeoecology of Africa 9, 160-202.

Weimarck H 1941. Phytogeographical groups, centres and intervals within the Cape flora. Lund Univ Arssk N F II 37, 1-143.

PHYTOGEOGRAPHY

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INTRODUCTION

In recent works both Takhtajan (1969) and Good (1974) allocated the rank of Kingdom to the Cape flora despite its small area on a world scale, thus according it phytogeographical importance equivalent to such a vast region as the Holarctic Kingdom, which encompasses the whole of the temperate and arctic northern hemisphere.

Capensis is bounded to the west and south by the coast, and to north and east principally by the Karoo-Namib Region (Werger 1978), together with some outliers of the Sudano-Zambezian (Werger and Coetzee 1978) and Afromontane Regions (White 1978). The Karoo-Namib flora penetrates into Capensis in the Little Karoo, an arid area between the coastal and inland mountains (Werger 1978). On mountains in the Knysna region, Capensis intergrades with the Afromontane flora, and several Cape species such as Berzelia intermedia, Diospyros glabra, Leucadendron eucalyptifolium and Protea cynaroides become prominent as one ascends from foothill forest to Mountain Fynbos (White 1978).

The broad phytogeographic demarcation of Capensis began in the last century when botanical travellers included "the region of the Cape flora" in their descriptions of vegetation formations and floristic kingdoms. Their descriptions were largely conjectural, and are of mere historical interest today. From the turn of the century, resident botanists like Bolus (1886, 1905) and Marloth (1906, 1908) began to describe and map the vegetation of South Africa. Delineation of the fynbos was gradually refined by Bews (1916), Pole Evans (1936), Adamson (1938a) and others, until finally Acocks (1953) recognized the main fynbos types accepted today. However, phytogeographical boundaries are still being debated (e g Axelrod and Raven 1978) and a clear picture will only emerge when the taxonomy and distribution of present floras, including lower plant groups, is known in detail.

CHARACTERISTICS AND AFFINITIES

The singular biogeographic features that led phytogeographers to give the Cape flora such a high status in their classifications include the great concentration of species, the high degree of endemism, the characteristic distribution patterns of typical elements, despite a general lack of species dominance, and the predominance of certain families and genera. The Cape flora "is noted for its richness in species, both in small areas and over its whole range" (Taylor 1978), and has been claimed as being one of the richest in the world for its size (Oliver 1977). For diversity at the community level (alpha diversity) Taylor (1972) has recorded 121 species of flowering plants in a single 100 m^2 quadrat in a homogeneous stand of Mountain Fynbos. This figure, although probably not the final tally, considerably exceeds the average level of alpha diversity in equivalent shrubland communities of mediterranean type ecosystems elsewhere (Kruger et al unpublished). Plant species richness at the landscape level, such as a mountain range (gamma diversity, Whittaker 1972), is much greater than that of south-western Australia, the richest floristic zone in that continent (Kruger 1977); while at the level of a floristic kingdom or province, Goldblatt's (1978) figure of 8 550 species of vascular plants in the Cape Floristic Region, compares well with the 7 000 given by McLarty (1952) for the whole of western Australia, an area about twenty times that of Capensis.

Two of the three families that are characteristic of the Cape flora, Restionaceae and Proteaceae, have a pronounced austral distribution. Both of them occur on all three southern continents and have very few representatives north of the equator. The third Cape family, Ericaceae, has no connections with either of the other two southern continents. Its subfamily Ericoideae that occurs in the Cape has a strictly north/south distribution. All three families have strong concentrations of taxa in Capensis; outliers occur on mountains in adjacent dry areas to the north, especially Namaqualand (Adamson 1938b), and also intermittently along the eastern highlands of the continent as far north as central Africa (Oliver 1977).

Many other typical Cape taxa have similar distribution patterns. In fact there are so many in the Drakensberg that both Killick (1963, 1978) and Edwards (1967) have described a type of "fynbos" for that area. But the floras of high mountains in southern and central Africa are incompletely known and intensive plant collecting is needed to provide data for a full phytogeographic study of these dispersal routes.

Families that are richest in genera at the Cape but widely distributed in other parts of the world include Fabaceae, Iridaceae, Rosaceae and Thymelaeaceae. In contrast, many taxa of high rank are endemic to the Capensis region or nearly so. These include Bruniaceae, Penaeaceae, Stilbaceae, Grubbiaceae, Roridulaceae and Geissolomataceae, the tribe Diosmae of the Rutaceae and large genera such as Aspalathus, Phylica, Muraltia and Cliffortia (Oliver 1977, Axelrod and Raven 1978, Taylor 1978). Weimarck (1941) found that, of 282 genera with their centre of origin in Capensis, 212 were endemic, and he estimated that more than 3 500 species out of the total of 4 200 that he surveyed were endemic. In examining local endemism, he found that the two westernmost centres together contained 45,5% of the total number of endemics represented within the "Cape proper."

Taxonomic studies show that both palaeoendemics, or relics, and neoendemics, or recently evolved species that are still limited to a small area, occur in the Cape flora. Both these types have local and/or disjunct distributions. The proteaceous species Orothamnus zeyheri, Mimetes hottentoticus and Leucadendron argenteum are, by virtue of their distribution and biology, considered to be palaeoendemics. Rourke (1972) reports vicariad groups of neoendemic Leucospermum species on coastal lowlands of the southern Cape and Levyns (1954) shows that several Muraltia species occupying the same coastal strip are also youthful endemics. From phylogenetic evidence, Oliver (1977) considers some species in the minor genera of the Ericaceae, and even some of the genera themselves, to be neoendemic. Marloth (1929) and Goldblatt (1972), among others, have attributed this local endemism and disjunction partly to the diverse topography of the region, in which the concomitant diversity of soils and local climates, and the appearance of new land surfaces along the coast, gave opportunities for recent speciation, and partly to the great age of the flora, members of which may have been able to survive climatic changes by retreating into favourable localities.

Weimarck (1941), Levyns (1938, 1952), Dahlgren (1963) and others have shown that typical families and genera of the Cape flora have a characteristic distribution pattern in which the highest numbers of species per area are concentrated in the western part of the region. Levyns (1952) went so far as to state it as a "rule that all genera of the Cape flora show a concentration in the south-west. Any apparent constituent, which does not show this particular pattern of distribution, may be suspected of being an invader." The Restionaceae, Proteaceae and most of the

Ericaceae show this pattern, as do the endemic families Bruniaceae and Penaeaceae and the larger genera *Cliffortia*, *Aspalathus*, *Phylica*, *Muraltia* and *Leucadendron* (Williams 1972).

On the other hand, genera like *Babiana* and *Osteospermum* that are common in Capensis have their maximum concentration in Namaqualand. Among other "apparent constituents" that do not show the typical south-western distribution are species of *Aloe*, *Erepsia*, *Carpobrotus*, *Crassula* and *Zygophyllum*. The presence of such species within the Cape flora, and the presence of fynbos outliers on high mountains in Namaqualand as far north as Springbok, suggest an intermingling of the Cape flora with those abutting it to the north.

In contrast, certain austral forest elements, also without the typical south-western concentration, occur within the Capensis region only as relict patches of forest in moist, sheltered habitats and not as constituents of fynbos. *Podocarpus*, *Cunonia*, *Platylophus* and *Curtisia* are examples (Levyns 1962). Though their presence suggests a previous wider distribution of forest, there is little evidence that they are becoming adapted to the typical rigorous habitats occupied by fynbos.

The Cape flora also contains elements that are found more commonly in more distant lands. The grass *Hyparrhenia hirta* has wide but disjunct distributions in the coastal Mediterranean, in east Africa and in southern Africa, linked only by high mountain outliers in the Sahara (Quézel 1978). Genera such as *Anemone*, *Rubus*, *Scabiosa*, *Geranium* and *Dianthus* have their main centres of concentration in the northern hemisphere. *Aloe*, *Euphorbia* and the Asclepiadaceae are prominent members of other African floras. *Gladiolus* is wide-spread elsewhere in Africa and beyond. *Rhus* and *Euclea* have many more species in subtropical forest, scrub and savanna than in fynbos (Taylor 1978).

Similarities at the generic level suggest comparatively recent dispersal and intermingling. Similarities at a higher taxonomic level suggest older affinities. Adamson (1958) considered that pairs of taxa like Selaginaceae (Cape) and Globulariaceae (Mediterranean), *Dimophotheca* and *Calendula*, *Lobostemon* and *Echium*, *Crassula* and *Sedum*, and *Widdringtonia* and *Tetraclinis*, provided evidence of a once widespread temperate flora that became fragmented as the climate changed and then evolved in isolation.

The affinity of the Cape flora with that of south-western Australia is striking but more remote than its affinities with northern hemisphere floras. The Thymelaeaceae, Haemodoraceae and Droseraceae are common to both continents, and the endemic Cape family Roridulaceae is closely parallelled by the Australian Biblidaceae. Diosmae (Rutaceae) of the Cape has its counterpart in the Australian tribe Boroniae (Bolus and Wolley-Dod 1904) and the genera Tetraria and Gahnia, and Phylica and Cryptandra are closely related (Adamsom 1958).

A picture emerges from this account of a present flora with high alpha and gamma diversity, a flora uniquely characterized by three widespread families and some endemic ones, and by many endemic taxa of lower rank, some young, some old, some widespread within the region, some restricted or disjunct in distribution. The flora has a high concentration of species in the west; it shows some close taxonomic affinities with abutting floras and with the central African mountain flora, obvious but more distant affinities with the flora of south-western Australia, and tenuous relationships with northern hemisphere floras. In all, the Cape flora is floristically and phytogeographically unique. Despite dispersals and interminglings, it appears to have been isolated for a long time and to have suffered vicissitudes that have encouraged speciation, radiation and hybridization at a singularly high rate.

ORIGINS OF FYNBOS

Such features suggest a long and varied history of geology and climate. On these grounds and because dominance by one or more species is a rare phenomenon in mature fynbos, the flora has been generally regarded as an ancient one (Marloth 1915, Bews 1925, Weimarck 1941, Levyns 1952, Adamson 1958, Dyer 1966). Yet despite general agreement on its age, there has been much controversy about the origin of the Cape flora. One school postulated an origin in the northern hemisphere, another in the southern, while yet a third contended that it originated somewhere in central Africa. Until very recently the third theory has seemed most plausible, mainly as a result of the perceptive work of Levyns (1938, 1952, 1958, 1964). She pointed out that very many members of the Cape flora, though they are concentrated in the Capensis region, show clear traces scattered throughout Africa, mainly on mountains as far north as Ethiopia. Proceeding southwards these "islands" become more frequent until south of the Swartberg all the scattered mountains of the Little Karoo have cappings of Cape plants, while the flora of the lowlands is entirely different (Levyns 1950). Levyns showed, too, that the more primitive members of Cape plants in many groups are to be found in mountain outliers within the tropics, whereas in the south-western Cape many of the species are advanced and occupy restricted geographical ranges. These distribution patterns suggest that a flora of the Cape type was once widespread in central Africa, and that this flora retreated southward when the climate became unfavourable in the north, leaving traces on the northern mountains and speciating in the favourable temperate conditions found in the south-western Cape.

This subject has been recently reviewed by Taylor (1978), who quoted further evidence suggesting that the presumed central African origin in fact represented a secondary centre of establishment for a flora that originated in austral lands. A review by Axelrod and Raven (1978), which appeared at the same time as Taylor's, presents evidence to support this theory. This evidence strongly suggests that dry summers are of recent origin in southern Africa and probably only appeared at the beginning of the Pleistocene some 2,5 million years ago. But already in the early Miocene, rapid speciation probably took place in South Africa with the broad warping and uplifting of the continent. Further study of fossil floras like those of Coetzee (1978a,b) is needed to substantiate this. At about this time increasing glaciation in Antarctica brought the cold water of the Benguela Current to the west coast, accentuating the trend to increased summer drought on the western land surfaces. Then, when strengthening high pressure systems brought this drier climate to the interior, sclerophyllous taxa that had lived earlier under summer and winter rain were adapting to increasingly dry summers. With dry summers spreading from the west, the taxa that required summer rain were gradually restricted eastward. This left the western environment open for the sclerophylls with tolerance to withstand summer drought, and many of those that survived in this new habitat had great opportunities for evolutionary radiation. This supports the findings of Levyns and others, mentioned earlier, that typical members of the Cape flora show a concentration of taxa and of endemics in the west.

But not all fynbos species originated in their present area. Axelrod and Raven (1978) postulate that even during the most recent climatic changes in the

Pleistocene, fynbos in its present area may have been restricted by the expansion of forest and other vegetation, and could then have been displaced to the north, into the regions now occupied by desert and semi-desert. At the end of the Tertiary when the area of dry climate expanded, fynbos would have retreated to its present area and, during this retreat, interchange between fynbos and isolated pockets of relict sclerophyll vegetation may have contributed directly and through hybridization to the overall diversity of the flora. Thus, the rich flora of the present Capensis region "may represent but a remnant of a much richer sclerophyllous flora that ranged over the present desert and steppe areas into the Pleistocene" (Axelrod and Raven 1978).

Though Axelrod and Raven's hypothesis is attractive, the diversity and high rate of speciation in fynbos may not simply be the result of mass plant migrations following climatic change. As Levyns (1963) has pointed out, a vegetation category, like fynbos, is not "a flock of sheep" but an association of taxa that extend and diminish their ranges, not collectively but individually, in response to different factors to which the taxa are variously adapted. For example, the fact that fynbos is largely restricted to nutrient-poor soils would preclude its movement en bloc into the Karoo-Namaqualand area, even though individual taxa may adapt to the richer soils there.

The pulse of alternating cooler and warmer, and at times wetter, climates during the Quaternary would also have contributed to the high diversity in the Cape flora. At times of moister climate, some taxa of the sclerophyllous Cape flora could have spread widely over the present Karoo region and speciated there. "As drier climate returned, the flora shifted coastward into its present area, bringing new taxa with them and leaving relict stands in moist situations" (Axelrod and Raven 1978). Thus, even during recent climatic changes in the Quaternary, the Cape flora may have been far more widespread (Levyns 1938 in Axelrod and Raven 1978), and has only been restricted to its present environment for a relatively short time.

An interesting feature in support of this view is that some Cape plants enter into a period of rapid vegetative growth towards the end of summer, at a time when water supplies in the south-western Cape are at their lowest. This strangely ill-adapted growth rhythm suggests that the ancestors of these plants "evolved in some place having a summer rainfall. The same phenomenon has been recorded for South Australia, where a similar change in climate is postulated to account for the same, apparently inexplicable, features of growth" (Levyns 1964). This suggests that the mediterranean climate is not ancient, but is so youthful that the plants have not yet fully adapted to it. Further research on South African plants is needed to clarify this phenomenon.

As stated earlier, a true mediterranean climate is present only in the western part of Capensis. It is this western part that was first colonized by primitive sclerophylls, and in the southwestern corner which has the highest rainfall and the most diverse topography, speciation has been most active, producing the greatest concentration of taxa and endemics. This rich southwestern centre can be regarded as the true home of the Cape flora from whence it has radiated. To the north its spread is limited beyond Van Rhynsdorp by an arid climate but eastward along the well-watered south coast it extends into the regions of non-seasonal and summer rain as far as Grahamstown. The eastern extension, having relatively low diversity and few endemics, is presumably younger than the western part. Fynbos would probably only have started colonizing this eastern area when the coastal temperate forest was reduced by a drying climate (see Acocks 1953, maps 1 and 2) but it has expanded its range faster within historic times due to the destruction of forest by man (Von Breitenbach 1972). Veld mismanagement is now encouraging its further spread eastward into mountain grassland (Trollope and Booysen 1971).

REFERENCES

Acocks J P H 1953. Veld types of South Africa. Memoirs of the Botanical Survey of South Africa 28, 1-192.

Adamson R S 1938a. The vegetation of South Africa. British Empire Vegetation Committee, London.

Adamson R S 1938b. Notes on the vegetation of the Kamiesberg. Memoirs of the Botanical Survey of South Africa 18, 1-25.

Adamson R S 1958. The Cape as an ancient African flora. Presidential Address, Section K (Botany), British Association, Glasgow. *The Advancement of Science* *15*, 118-127.

Axelrod D I and P H Raven 1978. Late Cretacious and Tertiary vegetation history of Africa. *Biogeography and ecology of southern Africa*. M J A Werger (ed). Junk, The Hague. pp 77-130.

Bews J W 1916. An account of the chief types of vegetation in South Africa, with notes on the plant succession. *Journal of Ecology* *4*, 129-159.

Bews J W 1925. *Plant forms and their evolution in South Africa*. Longmans, Green and Co, London.

Bolus H 1886. Sketch of the flora of South Africa. *The Official Handbook of the Cape of Good Hope*, Cape Town.

Bolus H 1905. Sketch of the floral regions of South Africa. *Science in South Africa*, Maskew Miller, Cape Town. pp 199-240.

Bolus H and A H Wolley-Dod 1904. A list of the flowering plants and ferns of the Cape Peninsula, with notes on some of the critical species. *Transactions of the South African Philosophical Society* *14*, 207-373.

Coetzee J A 1978a. Late Cainozoic palaeoenvironments of southern Africa. In: *Antarctic glacial history and world palaeoenvironments*. E M van Zinderen Bakker (ed). A A Balkema, Rotterdam. pp 115-127.

Coetzee J A 1978b. Climatic and biological changes in south-western Africa during the late Cainozoic. *Palaeoecology of Africa* *10/11*. A A Balkema, Rotterdam. pp 13-29.

Dahlgren R 1963. Studies on *Aspalathus*. Phytogeographical aspects. *Botaniska Notiser* *116*, 431-472.

Dyer R A 1966. Impressions on the subject of the age and origin of the Cape Flora. South African Journal of Science 62, 187-190.

Edwards D 1967. A plant ecological survey of the Tugela River Basin. Memoirs of the Botanical Survey of South Africa 17, 1-138.

Goldblatt P 1972. Iridaceae. Lectures on the Cape Flora at the University of Cape Town's Public Summer School, Jan-Feb. 1972. University of Cape Town.

Goldblatt P 1978. An analysis of the flora of southern Africa: its characteristics, relationships and origins. Annals of the Missouri Botanical Gardens 65, 369-436.

Good R 1974. The geography of the flowering plants. 4th Edition. Longmans, Green and Co, London. 557 pp.

Killick D J B 1963. An account of the plant ecology of the Cathedral Peak area of the Natal Drakensberg. Memoirs of the Botanical Survey of South Africa 34, 1-178.

Killick D J B 1978. The Afro-alpine Region. In: Biogeography and ecology of southern Africa. M J A Werger (ed), Junk, The Hague. pp 515-560.

Kruger F J 1977. Fynbos communities. Council for the Habitat. Conference on Mountain Environments of South Africa. Johannesburg, May 1976.

Levyns M R 1938. Some evidence bearing on the past history of the Cape Flora. Transactions of the Royal Society of South Africa 26, 401-424.

Levyns M R 1950. The relations of the Cape and Karoo floras near Ladismith, Cape. Transactions of the Royal Society of South Africa 32, 235-246.

Levyns M R 1952. Clues to the past in the Cape flora of to-day. South African Journal of Science 49, 155-164.

Levyns M R 1954. The genus Muraltia. Journal of South African Botany, Supplementary volume 2.

Levyns M R 1958. The phytogeography of members of Proteaceae in Africa. Journal of South African Botany 24, 1-9.

Levyns M R 1962. Possible Antarctic elements in the South African flora. South African Journal of Science 58, 237-241.

Levyns M R 1963. The origins of the flora of South Africa. Lantern 13(1), 17-21.

Levyns M R 1964. Migrations and origin of the Cape flora. Transactions of the Royal Society of South Africa 37, 85-107.

Marloth R 1906. The phytogeographical subdivisions of South Africa. Report of the British Association for the Advancement of Science for 1905, 589-590.

Marloth R 1908. Das Kapland. Gustav Fisher, Jena. 436 pp.

Marloth R 1915. The effects of drought and some other causes on the distribution of plants in the Cape region. South African Journal of Science 12, 383-390.

Marloth R 1929. Remarks on the realm of the Cape flora. South African Journal of Science 26, 154-159.

McLarty R 1952. Foreword. Gardner, Flora of Western Australia, 1,1.

Oliver E G H 1977. An analysis of the Cape flora. Proceedings of the Second National Weeds Conference of South Africa. Balkema, Cape Town & Rotterdam. 18 pp.

Pole Evans I B 1936. A vegetation map of South Africa. Memoirs of the Botanical Survey of South Africa 15, 1-23.

Quézel P 1978. Analysis of the flora of Mediterranean and Saharan Africa. Annals of the Missouri Botanical Gardens 65, 479-534.

Rourke J P 1972. Taxonomic studies on Leucospermum R Br. Journal of South African Botany, Supplementary volume 8.

Takhtajan A 1969. Flowering plants: origin and dispersal. Oliver and Boyd, Edinburgh. 310 pp.

Taylor H C 1972. Fynbos. Veld & Flora 2, 68-75.

Taylor H C 1978. Capensis. Biogeography and ecology of southern Africa. M J A Werger (ed). Junk, The Hague. pp 171-229.

Trollope W S W and P de V Booysen 1971. The eradication of macchia (fynbos) vegetation on the Amatole Mountains of the Eastern Cape. Proceedings of the Grassland Society of southern Africa 6, 28-38.

Von Breitenbach F 1972. Indigenous forests of the southern Cape. Journal of the Botanical Society of South Africa 58, 18-47.

Weimarck H 1941. Phytogeographical groups, centres, and intervals within the Cape flora. Lund Universitets Arsskrift Avd 2 Bd 37 Nr 5.

Werger M J A 1978. The Karoo-Namib Region. Biogeography and ecology of southern Africa. M J A Werger (ed). Junk, The Hague. pp 231-299.

Werger M J A and B J Coetzee 1978. The Sudano-Zambezian Region. Biogeography and ecology of southern Africa. M J A Werger (ed). Junk, The Hague. pp 301-462.

White F 1978. The Afromontane Region. Biogeography and ecology of southern Africa. M J A Werger (ed). Junk, The Hague. pp 463-513.

Whittaker R H 1972. Evolution and measurement of species diversity. Taxon 21, 213-251.

Williams M J 1972. A revision of the genus Leucadendron (Proteaceae). Contributions from the Bolus Herbarium 3, 1-425.

ZOOGEOGRAPHY

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INTRODUCTION

The zoogeography of fynbos is far less distinctive than the phytogeography. Werger (1978), in reviewing the zoogeographic status of southern Africa, shows that there is reasonable unity of opinion that the whole of southern Africa belongs to the Ethiopian region and that the fauna of the south-western Cape is not sufficiently distinct to justify recognition as a separate region. It is perhaps different enough to be recognised as a zoochorion of lesser rank. This, of course, is in marked contrast to the rank of Kingdom allocated to the Cape flora (Marloth 1908).

ENDEMISM

The greatest number of endemic animals is to be found amongst the invertebrates. Pinhey (1978) lists the Cape fynbos as one of the southern African areas richest in endemic Lepidoptera - particularly the diurnal Satyridae and Lycaenidae. Endrödy-Younga (1978) gives a long list of endemic species and many endemic genera which characterize the fynbos Coleoptera and Van Bruggen (1978) states that of the approximately 100 species of slugs and snails found in fynbos, about 60 are endemic to the area. Perhaps of greatest zoogeographic interest are the primitive relict groups found within the fynbos invertebrates. These relict groups represent the palaeogenic element of the fauna and include, amongst others, the Onychophora and Megaloptera, some Diptera, Orthoptera and Coleoptera. They show affinities with groups at the southern tips of other southern continents and are considered to be a legacy of Gondwanaland (Bigalke in press).

The south-western Cape can be considered to be a minor centre of endemism for the lower vertebrates. The zoogeography of the southern African vertebrates has been reviewed recently and will therefore only be mentioned briefly here (Bowmaker, Jackson and Judd 1978; Poynton 1978; Winterbottom 1978; Bigalke 1978 and in press).

Whilst not strictly part of the fynbos, the rivers of the southern Cape coastal region characteristically contain a depauperate fauna with a high proportion of endemic fishes. Of the 21 indigenous fishes which are restricted to fresh water and cannot disperse via the sea, 17 are endemic (Bowmaker et al 1978). This, together with the fact that the Cape Amphibia show a high degree of endemism, lends support to claims for the uniqueness of the fauna of the south-western Cape. Poynton (1964, 1978) suggests that the southern African Amphibia can be divided into two main centres - a 'Cape fauna' centred in the south-western Cape and a 'Tropical fauna' in the eastern tropical lowlands. In the 'Cape fauna', 19 of the 26 species and subspecies recognized by Poynton are endemic to the area.

Taxonomic problems and a paucity of up-to-date information make it difficult to form a clear picture of the species composition and distribution of fynbos reptiles. This is particularly true of the lizards where anything between 50 and 70 species and subspecies may occur in fynbos communities. The taxonomic arrangement laid out by FitzSimons (1943) requires extensive revision. FitzSimons (1962) records over 30 species of snakes from the western Cape with two endemic subterranean forms. It would appear that only a small proportion of the reptiles in the Fynbos Biome are actually restricted to it. One notable exception is the tortoise Psammobates geometricus, the only species of tortoise endemic to the south-western Cape (Greig and Burdett 1976).

Birds are by far the best known group of fynbos vertebrates. Although Moreau (1952) regarded the fynbos as a distinct avifaunal "district", Winterbottom (1978) feels that fynbos birds are far less distinctive than the lower vertebrates and the flora; of the 101 regularly occurring bird species, only six are endemic (Winterbottom 1972, 1978). Reasons for this scarcity of endemic birds have been examined by Cody (1975) and Winterbottom (1970) and appear in part to be due to the fact that the fynbos vegetation is not structurally unique and partly because the region has been in communication with large source areas with a comparable structure in the Karoo and highveld.

As with the birds, the fynbos lacks a distinctive mammalian fauna. Mammals endemic to the south-western Cape are the rodents Praomys verreauxi, Tatera afra, Acomys subspinosus, Bathyergus suillus and a gerbil found only on the Cape Flats but of still uncertain taxonomic status (possibly Gerbillurus mulleri, Schlitter pers comm); the insectivore Chrysochloris asiatica; and the antelope, Damaliscus dorcas dorcas, the extinct bloubok Hippotraqus leucophaeus and Raphicerus malanotis, considered by Bigalke (1978, p 1024) to be 'endemic to the South West Cape zone with a limited overlap into the southern Savanna'. It is only in this latter mammal, the Cape grysbok, that vegetation type appears to be critical (Manson 1974).

NEED FOR RESEARCH

It is readily apparent from literature on the fauna of the south-western Cape that a critical zoogeographic assessment of the fynbos fauna is not yet possible. The reasons for this are numerous but can generally be placed within three broad categories.

Firstly, distribution records for the fauna of fynbos are sparse and frequently contain large gaps - especially for the more mountainous parts of the south-western Cape where little serious systematic collecting has been attempted. With many species, repeated collecting in one area is necessary before a true picture of the faunal composition of the area can be obtained. For this reason it should always be borne in mind that the apparent restriction of certain taxa to the fynbos might well be an artefact produced by collecting methods. Bowden (1978) points out that an area with a rich and unique fauna tends to attract attention and stimulate a disproportionate amount of collecting and study - again producing an erroneous picture of the faunal composition relative to other areas. In a highly agricultural country such as South Africa, much research has been restricted to species of economic importance, again leading to undue emphasis being placed on a few taxa. It therefore appears that there is an urgent need for extensive and systematic collection of material in the fynbos. There is also a real need for a coordinating centre where the information obtained can be filed and thus made easily accessible to anyone involved in research on fynbos.

Secondly, severe limitations are imposed on zoogeographers by the lack of taxonomic knowledge of some groups, especially amongst the Invertebrata, and by the outdated and often confusing taxonomy of other groups such as the Reptilia. Again this is a field which is basic to our whole understanding of the zoogeography and ecology of the fynbos and is in urgent need of attention.

Thirdly, the factors primarily responsible for the distribution of the fynbos fauna are a matter of debate and uncertainty. Whereas the vegetation itself may well play a major role in the distribution of many of the invertebrates, we have seen that this is almost certainly not true for the vertebrates - where only a few specialized feeders show distributions which can be unquestionably linked to the fynbos itself. Poynton (1964, 1969) suggests that temperature is a primary factor in the "dynamic patterning" of some species of Amphibia. He stresses the need for detailed studies on the environmental parameters required by individual species and states that at present there is no species of southern African amphibian about which we have adequate knowledge (Poynton 1978). The same can be said about the majority of the fynbos fauna.

Current research aimed at meeting these needs appears to be concentrated largely on the fynbos vertebrates. Here, systematic collecting of material by museums, universities and the Departments of Nature Conservation and Forestry in the Cape is slowly filling in gaps in the distributional records. Research is also being carried out on the taxonomy of problematic groups, particularly within the Reptilia. Work on the fynbos invertebrates is severely limited by a shortage of manpower and funds and it is generally still true to state that only species of known economic importance are receiving adequate attention.

REFERENCES

Bigalke R C 1978. Mammals. Biogeography and ecology of southern Africa. M J A Werger (ed). Junk, The Hague.

Bigalke R C (in press). Aspects of vertebrate life in fynbos, South Africa. Ecosystems of the world. Vol 9. Heathlands and related shrublands. R L Specht (ed). Elsevier, Amsterdam.

Bowden J 1978. Diptera. Biogeography and ecology of southern Africa. M J A Werger (ed). Junk, The Hague.

Bowmaker A P, P B N Jackson and R A Jubb 1978. Freshwater Fishes. Biogeography and ecology of southern Africa. M J A Werger (ed). Junk, The Hague.

Cody M L 1975. Towards a theory of continental species diversities. Ecology and Evolution of Communities. M L Cody and J M Diamond (eds). The Belknap Press, Harvard.

Endrödy-Younga S 1978. Coleoptera. Biogeography and ecology of southern Africa. M J A Werger (ed). Junk, The Hague.

FitzSimons V F M 1943. The lizards of South Africa. Transvaal Museum Memo 1, 1-528.

FitzSimons V F M 1962. The snakes of southern Africa. Purnell, Cape Town, Johannesburg.

Greig J C and P D Burdett 1976. Patterns in the distribution of southern African terrestrial tortoises (Cryptodira : Testudinidae). Zoologica Africana 11, 249-273.

Manson J 1974. Aspekte van die biologie en gedrag van die Kaapse grysbok, Raphicerus melanotis Thunberg. M Sc Thesis. University of Stellenbosch.

Marloth R 1908. Das Kapland. Jena: Gustav Fischer. 436 pp.

Moreau R E 1952. After Winterbottom (1978).

Pinhey E 1978. Lepidoptera. Biogeography and ecology of southern Africa. M J A Werger (ed). Junk, The Hague.

Poynton J C 1964. The Amphibia of southern Africa: a faunal study. Annals of the Natal Museum 17, 1-334.

Poynton J C 1969. Optimum temperature and amphibian distribution in south-east Africa. Palaeoecology of Africa 4, 161-162.

Poynton J C 1978. The Herpetofauna. Biogeography and ecology of southern Africa. M J A Werger (ed). Junk, The Hague.

Van Bruggen A C 1978. Land Molluscs. Biogeography and ecology of southern Africa. M J A Werger (ed). Junk, The Hague.

Werger M J A 1978. Biogeographical division of southern Africa. Biogeography and ecology of southern Africa. M J A Werger (ed). Junk, The Hague.

Winterbottom J M 1970. Climate and range changes of birds in the south-west Cape. Palaeoecology of Africa 4, 150-153.

Winterbottom J M 1972. The ecological distribution of birds in southern Africa. Monographs of the Percy FitzPatrick Institute of African Ornithology 1, 1-82.

Winterbottom J M 1978. Birds. Biogeography and ecology of southern Africa. M J A Werger (ed). Junk, The Hague.

PLANT ECOLOGY

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INTRODUCTION

A description of the vegetation of the Fynbos Biome is necessarily incomplete because the formation categories and plant communities have not yet been adequately described. Acocks (1953) notes that to divide Mountain Fynbos into two Veld Types (VT), 69 and 70, is a simplification like "..... dividing the tropical vegetation (of South Africa) into grassveld and bushveld .....". With regard to Coastal Fynbos, he contends that a proper study would compel recognition of three veld types: the fynbos of the limestone in the Bredasdorp area, the dwarf fynbos of the Elim flats, and the remainder. The best that can be achieved at this stage is a description of typical fynbos plant forms, and of apparently representative communities of major fynbos types, as well as a discussion of some prominent functional features demonstrating responses of species and communities to their environments.

The major vegetation types of the Fynbos Biome are discussed briefly in the introductory chapter. No single variable has proved useful in defining each of these types. As a result, Table 1 has been compiled from definitions and descriptions by Acocks (1953), Taylor (1978), Kruger (1979), Boucher and Moll (in press) as well as from unpublished information.

MOUNTAIN FYNBOS

Mountain Fynbos, like the other true fynbos type, Coastal Fynbos, is distinguished physiognomically by the constant presence of two growth forms, ericoid shrubs, and restioid herbs, and the frequent presence of proteoid shrubs (Taylor 1978). Ericoid shrubs are dwarf and low evergreen shrubs with hard, narrow rolled leaves: Erica is

Table 1. Physical environmental variables and community features characteristic of the major Fynbos Biome vegetation types

	Mountain Fynbos	Coastal Fynbos	Coastal Renosterveld	Strandveld
Physiography	Foothills, slopes and crests of mountains of the Cape Folded Belt, on granites, shales, sandstones, and quartzites from near sea-level to about 2 250 m.	Sand plains, dunes and low rolling limestone hills of the Coastal Forelands, from near sea-level to about 150 m.	Slightly undulating to lightly dissected lowlands mainly on formations of the Malmesbury, Klipheuwel and Bokkeveld Groups, and Cape granite hills, from near sea-level to 400 m.	Sand plains, dunes, low limestone and granite hills along the littoral of the Coastal Forelands, from near sea-level to about 150 m.
Rainfall	250-3 300 + mm yr^{-1}	200 - 500 mm yr^{-1}	300 - 600 mm yr^{-1}	200 - 300 mm yr^{-1}
Soil	Leached, normally greyish, sands to sandy loams: lithosols, podzolics and podzols. Very acid (pH 3,5 to 5,5). Structureless sub-soil horizons.	Deep, usually greyish, slightly alkaline to acid (pH 6,0 to 8,0) medium sands; slightly alkaline to neutral lithosols on limestones; usually leached but sometime base-saturated structureless sub-soil horizons.	Clay-loams or clays, often gravelly, reddish, base saturated or super-saturated, slightly acid to neutral, often shallow. Sub-soil horizons usually structured.	Deep neutral to alkaline medium reddish sands; shallow lithosols on granites and limestones.
Diagnostic growth forms	Restioid herbs; ericoid and proteoid shrubs; (few spring annuals except in semi-arid situations).	As for Mountain Fynbos.	Low cupressoid, narrow-sclerophyllous and narrow-orthophyllous shrubs; deciduous perennial and annual grasses; succulent dwarf shrubs.	Many: broad-sclerophyllous shrubs, evergreen succulent shrubs, drought-deciduous succulent shrubs, spiny shrubs, spring annuals.
Special life forms	Acaulescent and rhizomatous dwarf shrubs		*Elytropappus rhinocerotis*	
Characteristic leaf forms	Isobilateral broad-sclerophyll (proteoid leaves): ericoid (small, rolled, with stomata in grooves): narrow-sclerophyll including pinoid: membranous-caducous or aphyllous (restioid).	As for Mountain Fynbos.	Cupressoid; small broad-sclerophyll often with resinous surfaces; soft felted narrow-orthophyll; broad-orthophyll.	Broad-succulent; narrow-succulent; succulent-deciduous; broad-sclerophyll.
Characteristic functional features	Evergreenness; complex seasonality; adaptations to fire regime.	As for Mountain Fynbos.	Evergreenness in dominants; spring herbaceous flora.	Drought-deciduous features; succulence. Spring herbaceous flora.

a typical example, but the category includes Rhamnaceae (some *Phylica* spp), Asteraceae (e g *Stoebe*) and others. The restioid herbs are aphyllous, evergreen, tufted or scapose graminoid herbs usually in the Restionaceae. Proteoid shrubs are medium to tall broad-sclerophyllous shrubs with hard, leathery and usually isobilateral leaves: members of *Protea* are the obvious examples.

Acocks (1953) distinguished between Macchia (VT 69) and the more eastern False Macchia (VT 70), apparently on geographical grounds but also because he felt the latter category comprised communities transitional to grassland, or to forest. Neither Taylor (1978) nor Kruger (1979) has upheld this distinction and it will not be retained here.

Life forms

Trees are rare in Mountain Fynbos but include some notable endemics. The cupressoid trees *Widdringtonia cedarbergensis* and *W schwarzii* occasionally form open forests or woodlands but populations normally consist of very few individuals restricted to special habitats such as cliffs, apparently where fires are less frequent. Both species have restricted distributions, the former occurring over some 250 km^2 in the Cedarberg and the latter as scattered, isolated populations in the Kouga and Baviaanskloof mountains. In both cases, trees are killed relatively easily by fire, and rely on seed for survival. These trees appear ill-adapted to the fynbos environment; Hubbard (1937), Lückhoff (1963, 1971) and Andrag (1977) describe their biogeography, ecology and conservation.

Leucadendron argenteum, a proteoid tree, forms a low sparse woodland with fynbos understorey on cool, moist eastern and poleward slopes with granite or shale soils on the Cape Peninsula and in the Stellenbosch area. Fruits are retained in cone-like heads "for some years" after ripening (Williams 1972). Seedlings establish readily after a burn and many adults survive, protected by thick corky bark. Thus populations in burnt areas comprise several distinct cohorts.

A few other species form small trees under favourable conditions. These include *Heeria argentea*, *Maytenus oleoides*. Each has protective bark and the capacity to re-sprout from epicormic buds. *Olea africana* reaches the stature of a tree where the vegetation is long protected against fire, as does *Widdringtonia nodiflora* (= *W* cupressoides). Three species of small rosulate trees are found occasionally in specialised habitats, Aloe plicatilis and A ferox in the south, and Encephalartos longifolius in the extreme east.

Riparian communities are dominated by species which form small trees where fire is excluded for 20 years or more. Such species include Metrosideros angustifolia, Podalyria calyptrata, Psoralea pinnata and Salix mucronata. Others, such as Brabejum stellatifolium, grow tall but do not lose the shrub habit.

Shrubs constitute the synusia richest both in species and in growth forms. Tall shrubs (taller than 2 m) are predominantly of three kinds: broad-sclerophylls, mainly of the Proteaceae; broad-sclerophylls with dentate margins (Leucospermum, Cliffortia) or dissected form (Paranomus) and often spiny (Cliffortia); narrow-sclerophylls, usually with pinoid rather than ericoid leaves (Bruniaceae and Aspalathus). The flora of this synusia is relatively small and the upper stratum of scrub and tall-heath communities is usually dominated by one or two species. Taylor (1978) lists some of the typical species and describes their distribution. Mature broad-sclerophylls normally reach a height of about three to four metres, but some such as Protea mundii may reach six or seven metres. Crowns may be slender to somewhat sphaeroid, depending on population densities, but are mostly regular with shoots that ascend at an acute angle, reflecting their sympodial, multifurcate branching habit. Species are normally microphyllous, sometimes mesophyllous (Protea arborea, P lorifolia), the leaves entire (Protea, Leucadendron, Maytenus) or nearly so (Leucospermum), and set at an angle to the branch, curving upwards. Leaf surfaces may be glabrous, hairy, coriaceous or glaucous.

Tall shrubs with dentate or lobed leaves occur unpredictably, usually as a minor component of any community, but some, such as Cliffortia ruscifolia (Adamson 1938b), may be locally dominant. Rhus angustifolia and R tomentosa form tall, multistemmed shrubs with compound broad-sclerophyllous leaves; they perhaps belong to a different category of sclerophylls, since their leaves are retained on the plant for a little more than a year. There are also some broad-orthophyllous shrubs, such as Chrysanthemoides monilifera, which are evergreen, but with short-lived leaves.

Table 2. Dimensions and leaf characters of selected broad-sclerophyllous shrubs from the Mountain Fynbos (mean values with standard deviations)1/

	Protea repens (n = 20)	Leucadendron rubrum (male) (n = 10)	Leucadendron rubrum (female) (n = 10)	Leucadendron laureolum (male) (n = 10)	Leucadendron laureolum (female) (n = 10)
Age (yrs)	approx 5	5 & 5 mnths	5 & 5 mnths	approx 20	approx 20
Mean ht (m)	1,39 ± 0,23	1,33 ± 0,16	1,35 ± 0,12	1,06 ± 0,13	2,15 ± 0,13
Mean crown area (m^2)	0,56 ± 0,37	0,24 ± 0,13	-	2,83 ± 0,53	1,25 ± 0,23
Mean stem diameter (cm)	3,00 ± 1,32	2,0 ± 0,4	2,2 ± 0,4	6,10 ± 2,16	5,9 ± 1,63
Mean mass per plant (gm^{-2})	2030 ± 1488	1852 ± 396	-	1486 ± 344	3194 ± 629
Mass of plant components as a proportion of total					
Leaves	30	41	37	29	23
Current shoots	3			6	4
Branches	45	56	46	56	43
Main stem				8	8
Reproductive organs	23	3	17	0	23
Mean area of leaf (mm^2)	413 ± 120	57 ± 11	220 ± 29	564	809
Leaf area index	-	-	-	2,5 ± 0,3	3,6 ± 0,3
Mean no of growing points per unit crown area in m^2	107 ± 88	-	-	-	-

1/ Data from a biomass analysis of random individuals of species populations at Jonkershoek, Zachariashoek and Kogelberg, respectively.

Tall narrow-sclerophyllous shrubs are usually dominant or prominent on phreatic sites and cool slopes of the southern mountains: species of Bruniaceae, such as Berzelia lanuginosa and Brunia alopecuroides, are typical. Mature Bruniaceae of this form have erect, slender stems with small tufted crowns of fine shoots and short pinoid leaves. Similar narrow-sclerophylls occur among the mid-height shrubs (1-2 m tall) and include Ericaceae such as Erica patersonia, E sessiliflora and E versicolor, Proteaceae such as Paranomus and Spatalla spp, and Fabaceae (Aspalathus spp), as well as a number of other taxa. Narrow-sclerophylls tend to increase in importance with increasing elevation.

The synusia of mid-height shrubs (1-2 m tall) contains forms like those among tall shrubs, and this is therefore not discussed further here except to note that it is sometimes relatively rich.

Table 2 summarises data descriptive of some broad-sclerophyllous shrub forms.

Low shrubs (25-100 cm tall) form a heterogeneous synusia, rich in species and growth forms. The most common of these, and the most characteristic type of shrub in the fynbos, is the low, single-stemmed, bushy, ericoid shrub, of which members of the Ericaceae and such genera as Metalasia and Stoebe (both Asteraceae) and Phylica (Rhamnaceae) are typical. Narrow-sclerophyllous, non-ericoid shrubs of the same form may also be prominent: various species of Rutaceae and Aspalathus are examples. These single-stemmed shrubs regenerate after fire from seed only. Communities are often dominated by one or two species of this form (examples are Erica demissa, Martin 1965 and Erica hispidula, Kruger 1972). Another form, Stoebe plumosa, with unique scale-like foliage, forms bushy sprawling mats, especially in certain Protea arborea communities when fire has been absent for upwards of eight years; an above-ground biomass of 10 - 12 tonnes ha^{-1} has been measured for Stoebe in such stands (Kruger 1979).

Another distinctive form consists of multistemmed low shrubs, and includes species that regenerate after fire by sprouts from lignotubers or root crowns. Some examples are Leucadendron salignum and other species of Leucadendron; Leucospermum mundii and Grubbia tomentosa and others (broad-sclerophyllous); Psoralea spp (compound broad-sclerophyllous); Erica coccinea, Retzia capensis and Phylica spp (ericoid) and Nebelia paleacea, Berzelia abrotanoides and species of the Rutaceae (narrow-sclerophyllous).

A common element of many communities, especially those on relatively fertile soils, is a group of sub-ligneous suffrutescent shrubs, with flowering shoots and foliage that die back annually in late summer to leave a low, perennial, rather woody, shrub body: examples are species of the genera Helichrysum and Helipterum, as well as Osteospermum junceum and other members of the Asteraceae. These shrubs occur in greatest abundance during the interval ending about eight years after fire.

In many communities the low shrub synusia is the most diverse, both with respect to number of species and to variety of forms. Most striking is the wide array of leaf forms, ranging from ericoids and other narrow-sclerophylls, to typical proteoid forms, and to the variety of soft, felted leaves in the suffrutices. Evergreen species dominate but the drought-deciduous shrubs Asparagus thunbergianus, Montinia caryophyllacea and Rhus rosmarinifolia are sometimes prominent. Shrubs with spiny leaves are frequent (eg Muraltia spp), and those with spiny stems (Asparagus spp) occasional.

Kruger (1979) presents a succinct account of the dwarf shrubs and other chamaephytes of the fynbos; his text is quoted extensively below:

"A wide variety of growth forms is included in this synusia. True dwarf shrubs of the Ericaceae, Rhamnaceae (Phylica) and others occur in most communities but dominate only in a few extreme habitats." Some of these are single-stemmed dense bushy shrubs, whereas others are multistemmed (resprouting from rootstock) with sparse crowns: Martin (1966) provides useful illustrations and descriptions. Marloth (1902) has noted the frequency of compact, accumbent, and procumbent shrubs (and other alpine growth forms) on high peaks in exposed situations at elevations in excess of about 1 800 m, but there is no true alpine or sub-alpine zone (Adamson 1938a). Shrubs of this form may be found at elevations of around 500 m (cf Erica banksia, E parvula) and procumbent shrubs, especially in the Fabaceae (Aspalathus, Indigofera) are common on sandy flats after fire.

Proteaceae are represented by acaulescent rosette shrubs (Protea scolopendriifolia), rhizomatous or reptant species (P acaulos) and low, circular spreading shrubs (Protea witzenbergiana) - these are often pollinated by non-flying mammals (see below). Succulent dwarf shrubs (Mesembryanthemaceae, Crassula) are present after fire in Mountain Fynbos (Adamson 1935), or as a permanent component on exposed rocky situations and in Arid Fynbos communities. As in the low shrub synusia, suffrutescent semi-shrubs, especially of the Asteraceae and Selaginaceae, are sometimes frequent, as are semi-parasitic dwarf Thesium and Thesidium species. Diffuse caespitose or spreading herbs (Carpacoce) and creeping herbs (Centella) may sometimes be abundant, especially in wet communities. Leaf morphology is highly variable, but narrow-sclerophylls tend to dominate.

Graminoid herbs and other hemicryptophytes are often the most prominent, and invariably an important, component of Mountain Fynbos communities. This group is usually very rich in species except in dense, old closed-scrub where lower strata are suppressed. "It is the synusia which most clearly distinguishes fynbos from its Mediterranean and New World analogues" (Kruger 1979).

Most important of the herbaceous forms are the graminoid and restioid herbs. Grasses and sedges, including typical genera like Pentaschistis, Merxmuellera and Ehrharta (Poaceae) and Tetraria and Ficinia (Cyperaceae), are present in all communities and though sometimes sparse are often relatively important. A great range of forms occurs, from large tussocks nearly 2,0 m tall (Merxmuellera cincta), through tufted forms of various sizes, to rosette and scapose grasses. Species of Tetraria with large tufts of slender leaves up to 0,5 m tall and culms to 2,0 m and more, are characteristic of many fynbos communities of humid habitats in the Outeniquas and Tsitsikamma (Phillips 1931). Tetraria thermalis, with a sprawling complex of tufts of broad glossy leaves up to 2,0 m in diameter, is typical of highly leached, well drained lithosols on sandstones in the area between Jonkershoek and Bredasdorp and on Table Mountain (Kruger 1974, Kruger 1979, Taylor 1978, McKenzie, Moll and Campbell 1977). These hemicryptophytes are usually evergreen but are sometimes only seasonally green.

Restioid herbs are evergreen hemicryptophytes with cylindrical photosynthetic stems, and leaves reduced to membranous sheaths; however the sterile stems in the Restionaceae sometimes have a complex structure and resemble foliage (Pillans 1933). Members of the Restionaceae dominate this category, but some Poaceae (eg Ehrharta ramosa), Cyperaceae (eg Neesenbeckia punctoria) and perhaps Iridaceae (Bobartia spp) may be included.

There is a great variety of form in restioid herbs. The extreme is the bamboo-like

Cannamois virgata which, in the Langeberg and elsewhere, forms loose tufts with erect shoots up to 3,0 m tall or more. In arid situations, densely rhizomatous species of Restionaceae like *Cannamois dregei,* with erect stems almost 1,0 cm thick, form conspicuous loose clumps up to 2,5 m high, while *Restio fruticosus* forms tufts with stems as high as about 2,0 m. Most restioid herbs are about 40 to 100 cm tall, and form scapose plants (*Restio gaudichaudianus*), rosettes (*Thamnochortus* spp), tufts (*Chondropetalum hookeranum*), and a variety of other forms, depending on whether rhizomes are stoloniferous (*Hypodiscus willdenowia*) or densely concentrated so that stems form open tufts (*Elegia juncea* and *Chondropetalum mucronatum*). Some species, such as *Restio perplexus* and *Hypolaena crinalis,* form hummocks in bogs and in certain high-elevation communities.

The restioid growth form dominates many communities, especially at high altitudes and on sites that are alternately waterlogged and arid each year (Kruger 1979, Taylor 1978, Figure 10). According to Kruger (1979), "Grasses tend to increase in importance with increasing soil fertility and increasing proportion of summer rainfall. Toward the east they tend to dominate the synusia." These trends are reinforced by frequent burning (e g Van Rensberg 1962).

There is a wide variety of perennial forbs in Mountain Fynbos, but in terms of numbers and biomass they are seldom of much importance in the community. Though geophytes are typical of all the mediterranean climate ecosystems (Schimper 1903) they are more important in fynbos than elsewhere, both in terms of absolute numbers of species and of relative abundance. Specht and Rayson (1957), for example, list 14 geophytes in 76 plant species sampled from Dark Island Heath, South Australia. Mooney and Parsons (1973) list 34 geophytes in a total of 517 plant species at San Dimas, southern California. Van der Merwe (1966) lists 68 in a native flora of 418 species in Swartboschkloof, Jonkershoek. They are abundant in some communities. Kruger (unpublished) estimated 3,2 plants (ramets) per square metre in a "medium" population and 15,3 plants per square metre in a "dense" population of *Watsonia pyramidata* at Jonkershoek. Total live biomass amounted to 75 and 461 g m^{-2}, respectively.

There is little character convergence among fynbos geophytes, which exhibit considerable heterogeneity with regard to leaf form (compare *Oxalis* with *Watsonia* and the *Orchidaceae*), leaf placement (compare *Haemanthus* with *Watsonia*) and seasonality (Kruger in press b). The predominance of cormaceous and rhizomatous species with erect strap-shaped leaves, and of bulbous species also with relatively erect leaves reflects the predominance of the Iridaceae and the Liliaceae, although more than 12 families are in fact represented in fynbos geophytes. Some do not fit the standard definition of geophyte, since they are evergreen (e g Aristea spp).

Annual herbs are absent or scarce in almost all Mountain Fynbos communities, only being found in abundance in the first season after fire. Examples are Heliophila crithmifolia, Sebaea exacoides, Ursinia anthemoides and Manulea cheiranthus (Adamson 1935).

Among the climbers, woody lianes are absent, except that Secamone alpini may occur in communities adjacent to dry forest. Herbaceous climbers may be quite frequent, and are usually seasonally green (Cyphia volubilis and Microloma tenuifolia, but see below).

Among the parasites, Cassytha ciliolata is a common climber in shrublands of lower elevations and may sometimes dominate. Cuscuta nitida is found occasionally but does not spread. A variety of root-parasites in the genera Harveya, Hyobanche, Mystropetalon and others are frequent but are seldom encountered. Cytinus spp (Rafflesiaceae) are found in certain habitats.

Plant formations

The structure of Mountain Fynbos plant communities varies considerably except in respect to density. Communities are normally dense with canopy cover in mature stands usually exceeding 75%. Some measures of structural variation are depicted in Table 3.

In their most complex form, stands comprise three more or less distinct layers (see Figure 1): an upper layer of proteoid shrubs, about 1,5 to 2,5 m high or more, sometimes closed but usually discontinuous; "a dense middle layer of ericoids, lower proteoids with smaller leaves and some large tufted (graminoid) herbs ....., and a ground layer of small shrubs, herbs, many geophytes and low restioids, often matted and wiry" (Taylor 1978). However, stratification is often much simplified (see below).

Table 3. Summary of community data for a range of Mountain Fynbos structural formations (from Kruger 1977b)[1]

Formations	Open-scrub		Tall shrubland with heath		Low open-heath		Low graminoid-heath		Low closed-herbland	
Elevation (m)	490		285		820		930		840	
Rainfall (mm)	1 600		1 600		950		950		950	
Total canopy cover %	95-100		95		80		95		95	
Total plant species	72		126		52		71		31	
	No of spp	R I[2]	No of spp	R I	No of spp	R I	No of spp	R I	No of spp	R I
Tall shrubs (2 m, evergreen)	21[3]	48,0	1	36,8	0	0	0	0	0	0
Low and mid-ht shrubs (0,25-2 m)										
Evergreen	25	46,5	45	34,8	17[3]	60,7	21[3]	48,8	5	2,7
Deciduous	2	+	3	3,6	0	0	0	0	0	0
Shrub and tree sub-total	29	94,5	49	75,2	17	60,7	21	48,8	5	2,7
Dwarf shrubs (evergreen)	7	+	10	0,6	4	+	13	+	2	0,4
Graminoid herbs	13	4,0	17	19,8	23	38,0	22	45,7	13	90,3
Geophytes	18	+	34	1,4	7	0,3	10	4,5	9	5,9
Other herbaceous perennials	3	+	7	0,4	1	+	5	0,5	2	+
Herbaceous perennials sub-total	34	4,0	58	21,6	31	38,3	37	50,7	24	96,2
Annuals	1	+	7	+	0	0	0	0	0	0
Succulent shrubs	0	0	2	+	0	0	0	0	0	0
Vines	1	+	0	0	0	0	0	0	0	0

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[1] All data for 20 x 50 m plots.

[2] R I = relative importance as percentage of total crown volume (sum of products of height and cover for each species). '+' denotes trace.

[3] Synusiae dominated by seed-regenerating shrubs.

Figure 1. Sparse broad-sclerophyllous shrubland with restioid understorey in Mountain Fynbos of the Kouga mountains. Prominent shrub is *Protea repens*, 1,5 to 2,0 m tall. Sparse intermediate shrub layer, 0,4 to 0,6 m tall, contains mainly Proteaceae (*Leucospermum*, *Leucadendron* and *Paranomus* spp) and occasional Ericaceae. Restioid layer, 0,4 to 0,7 m tall with approx 60% coverage, is dominated by *Hypodiscus* and *Cannamois* spp

Structural formations range from open woodlands through tall scrub to dwarf shrublands and low herblands, the names of the formations depending to some extent on the terms used to define structure. The location of these formations in the landscape is not always consistent but Taylor (1978), following Adamson (1938a), recognized two broad but diffuse vegetation zones, the proteoid and the ericoid-restioid zones, as well as the azonal hygrophilous fynbos. Kruger (1979) describes and discusses a range of structural formation categories within each of six broad habitat categories and illustrates examples of the formations with detailed analyses of stands in a range of communities. Martin (1965), Van der Merwe (1966), Jessop and Jacot Guillarmod (1969), Taylor (1969), Werger, Kruger and Taylor (1972), Kruger (1974), McKenzie *et al* (1977) and Boucher (1978) present detailed descriptions of a variety of community types from areas of differing size in the mountain landscape. Here the formations will be described briefly using Taylor's (1978) framework.

The proteoid zone is defined as that in which the proteoid shrub form predominates (Taylor 1978) and is found in the foothills, lower slopes and plateaus of the Cape Folded Belt mountains. "On poorly insulated slopes in the west, with a rainfall of about 500 to 1 000 mm yr^{-1}, this zone extends up to an altitude of 900 to 1 000 m. Rainfall generally varies from 500 to 1 000 mm yr^{-1}, but may reach 1 600 to 1 800 mm yr^{-1}. In the east, on cool slopes with a higher rainfall, the upper limit is lower; on hot northerly slopes it is higher" (Taylor 1978). Vegetation which has not been unduly disturbed consists of communities with three layers, but with great variation in the structure of each. Thus the upper, proteoid shrub layer

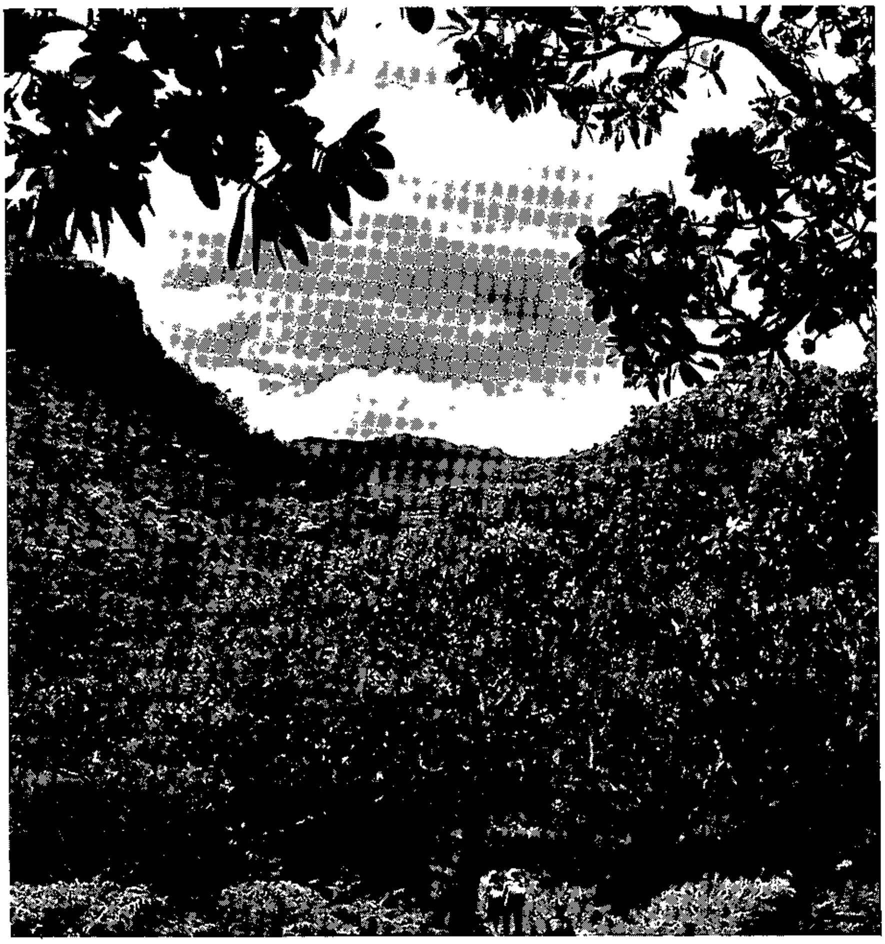

Figure 2. Open Protea arborea woodland - Waboomveld - in the Cedarberg. Here trees are 4 to 5 m tall with diameters up to 300 to 400 mm. Pteridium aquilinum in left foreground

ranges in cover from sparse to closed. The middle layer is usually quite dense, except in closed-scrub stands, but the relative importance of graminoid herbs, of restioids, and of low shrubs varies from nearly complete dominance by one to almost perfect codominance. The predominant formations of this zone are broad-sclerophyllous scrub or open-scrub communities with the upper stratum dominated by one, or sometimes two, species, often including Protea laurifolia, P neriifolia, P repens, Leucadendron laureolum, L gandogeri, and L eucalyptifolium. A common formation throughout this zone is Waboomveld, a sparse or open low woodland or shrubland, characterised by the Waboom, Protea arborea, and confined to a special if widespread habitat type (Figure 2). Taylor (1969, 1978), Werger et al (1972) and Kruger (1979) provide detailed information.

The proteoid zone is not continuous and low ericoid shrublands and other formations often transgress the boundaries. Taylor's ericoid-restioid zone is distinguished by the relative scarcity of the proteoid form and is a zone of low vegetation with communities dominated by ericoid shrubs, tufted restioid herbs, or a mixture of both. It is found on cool, humid to perhumid upper slopes, ridges, plateaus and summits of the mountains, on soils that are usually more acid and more highly leached than in the proteoid zone. Low ericoid shrublands may follow infertile substrates down to elevations of about 200 m. Some plant formations of the ericoid-restioid zone are illustrated in Figures 3 and 4.

Taylor's category of hygrophilous fynbos includes a wide range of communities in a diversity of habitats, each of which has soils that are wet or moist throughout the year. Along streams and rivers, riparian shrub communities are the rule and, if sheltered, grow to form a broad-sclerophyllous closed-scrub with a relatively simple structure. Perhaps the most common formation is that in which species like Brabejum stellatifolium and Metrosideros angustifolia form a continuous canopy about 5 to 6 m high, with sparse understories of lower shrubs and ferns. On exposed sites, tall plumose Restionaceae such as Restio subverticillatus, Elegia capensis and Leptocarpus paniculatus, are characteristic (Kruger 1979).

On humid, cool, south slopes of the southern mountains, a widespread mixed sclerophyllous scrub is the typical "hygrophilous" formation. It is tall, with an upper stratum 3 to 4 m high, but it sometimes reaches 7 m, characteristically consisting of a mixture of proteoid shrubs (e g Leucadendron eucalyptifolium) and narrow-sclerophyllous shrubs (Bruniaceae spp). The middle layer consists of a

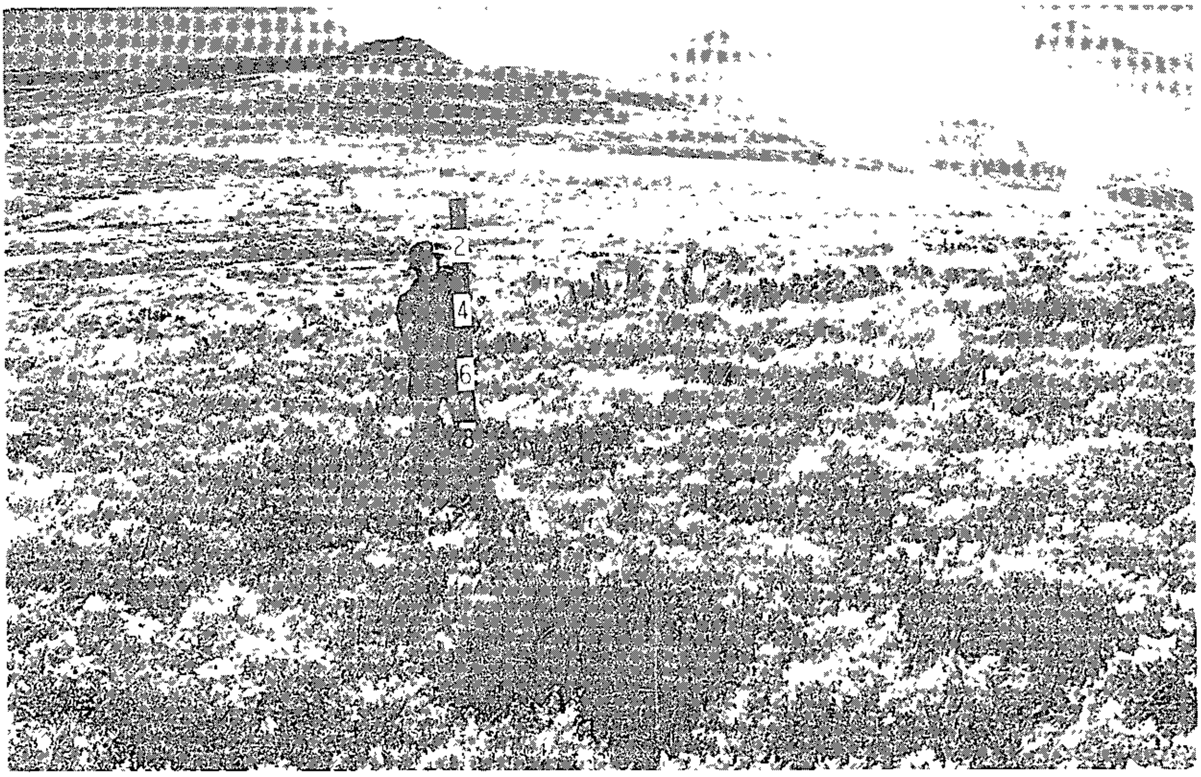

Figure 3. Low heathland in Mountain Fynbos of the southern slopes of the Langeberg near Heidelberg. Dominant species is Erica melathera. Staff is 2 m high. (Photo Department of Forestry)

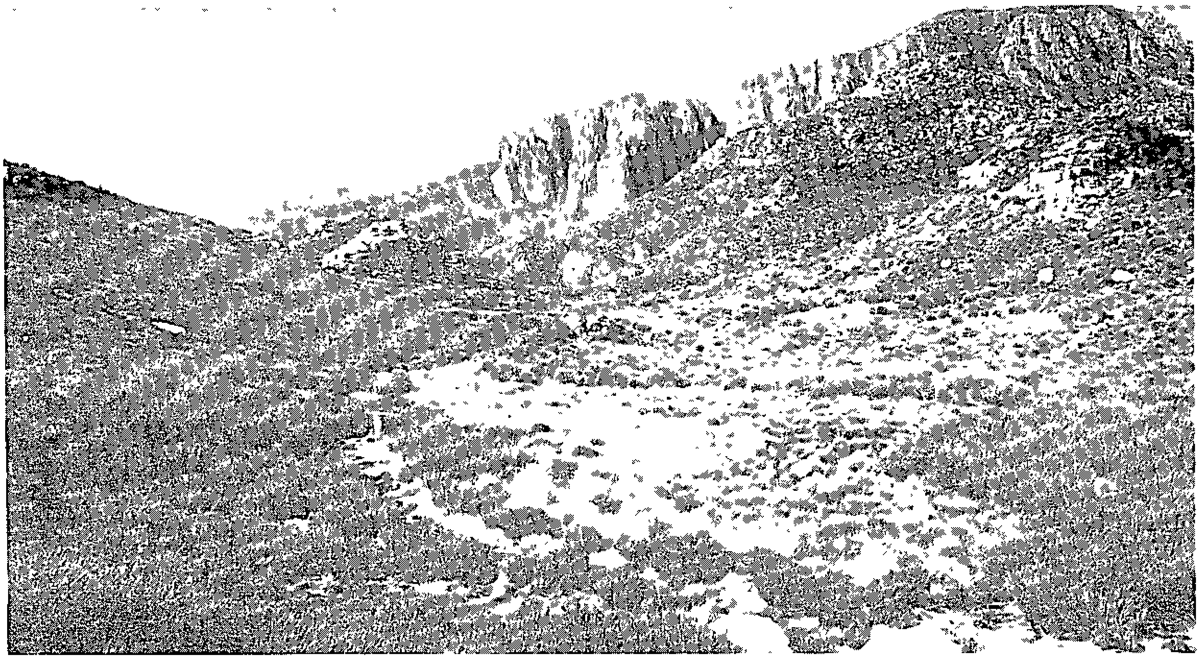

Figure 4. Restioid herblands in Mountain Fynbos of the Dwarsberg plateau, Jonkershoek at about 1 250 m above sea level (see Kruger 1979 for details). This site receives about 3 300 mm rainfall per year, the highest recorded in South Africa. Rain gauge is 1,2 m high

thicket of ericoid and other shrubs and tall graminoid and restioid herbs, whereas the lower layer of tufted hemicryptophytes, low shrubs and herbs is discontinuous. Phillips (1931) suggests that this type is seral in a forest succession; certainly its ecological features are not like those of other fynbos communities.

On mountain slopes which are otherwise well drained, local phreatic zones have a range of plant communities which diverge markedly in structure from surrounding communities. Among these types is one which is dominated by Osmitopsis asteriscoides, a slender, erect, aromatic, broad sclerophyllous shrub and Elegia thyrsifera, a loosely clumped rhizomatous restioid; the canopy is usually 2 to 3 m high. Elsewhere, especially on the Cape Peninsula and in the Hottentots-Holland Mountains and hills eastward to Bredasdorp, Bruniaceae dominate on phreatic sites. Often however, and possibly due to excessive waterlogging, shrubs are absent or sparse and Restionaceae and Cyperaceae dominate mid-height and low herblands. The communities on level ground in Figure 4 are examples.

ARID FYNBOS

Arid Fynbos, a poorly known sub-type of Mountain Fynbos, is often an intruder into Karoo zones and retains its territory only because of the hydrologic properties of the sandy substrate on which it occurs (Kruger personal observation).

It is recognized on the basis of communities with characteristic structural features, such as a sparse canopy with cover usually less than 50% and poorly discernible stratification (Adamson 1938a, Taylor 1978). Arid Fynbos formations are found on deep sands and on rocky mountain slopes of the interior, roughly between the 250 and 400 mm isohyets, and on soils derived from Table Mountain sandstones, Witteberg quartzites, and, in the Khamiesberg, granite (Kruger 1979).

Life-forms are like those of Mountain Fynbos. Ericoid shrubs are less common, as are evergreen graminoid herbs. By contrast, seasonal annuals are prominent, with more species, a greater biomass, and regular appearance in winter and spring in any community. Seasonal geophytes are more conspicuous than in Mountain Fynbos, but are apparently not present in greater abundance or diversity (1979); evergreen geophytes are absent. Most grasses are seasonal, either as annuals or as deciduous perennials. Drought-deciduous shrubs such as Rhus incisa, Wiborgia

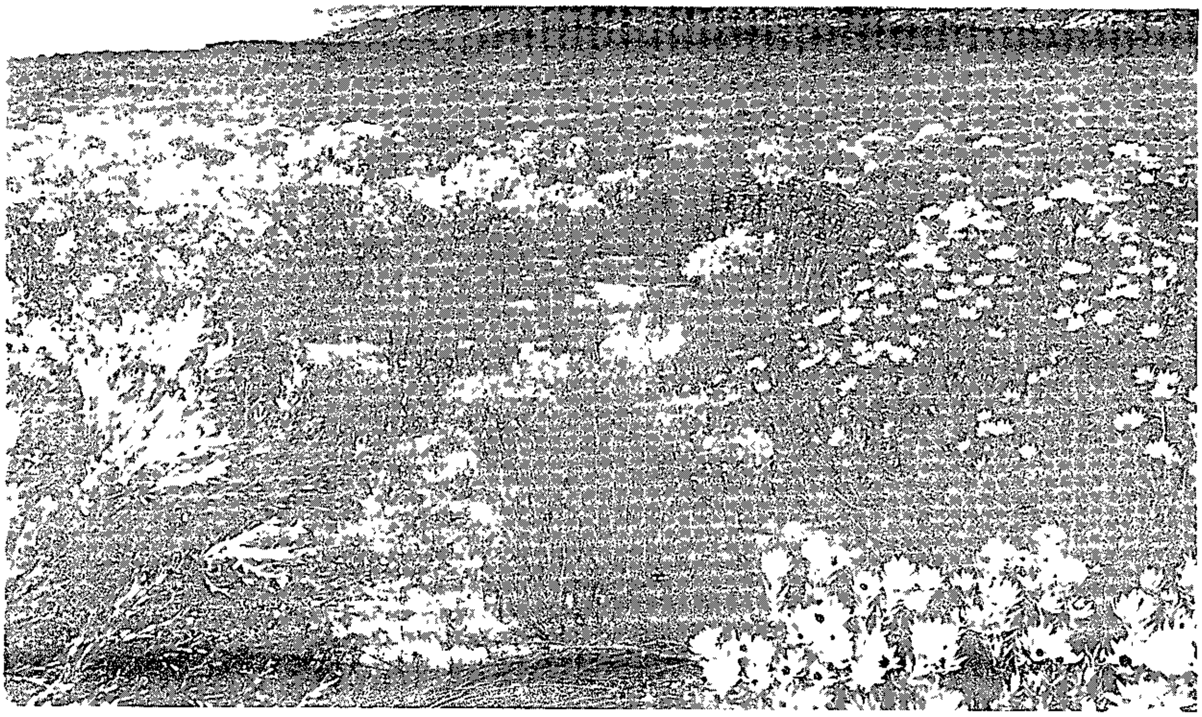

Figure 5. Sparse sclerophyllous shrublands on deep sand north of Citrusdal (see Kruger 1979 for details). Prominent shrub in right and left foreground is Leucadendron loranthifolium and that at right, middle, is L pubescens, both 1,2 to 1,6 m tall. Note abundant annuals (Ursinia sp)

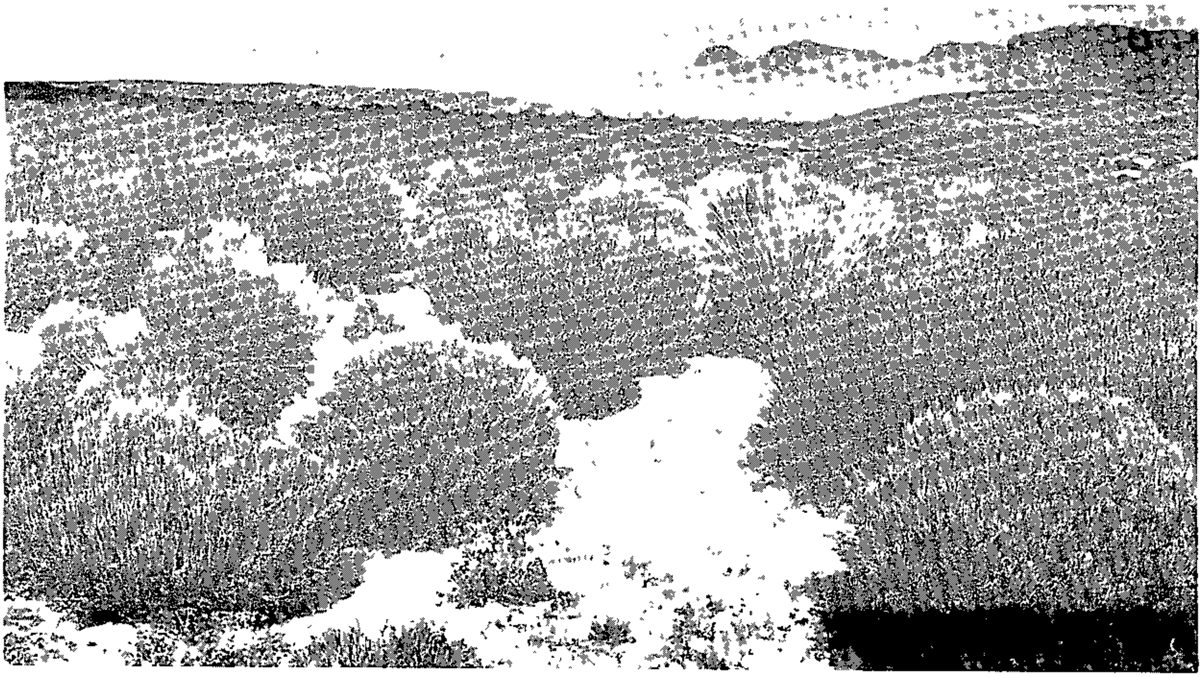

Figure 6. Sparse mixed community of Arid Fynbos on shallow sands north of Wuppertal. Note globose shapes of shrubs (Passerina sp prominent) and of tufted restioids (Willdenowia striata), all about 0,5 to 0,8 m tall

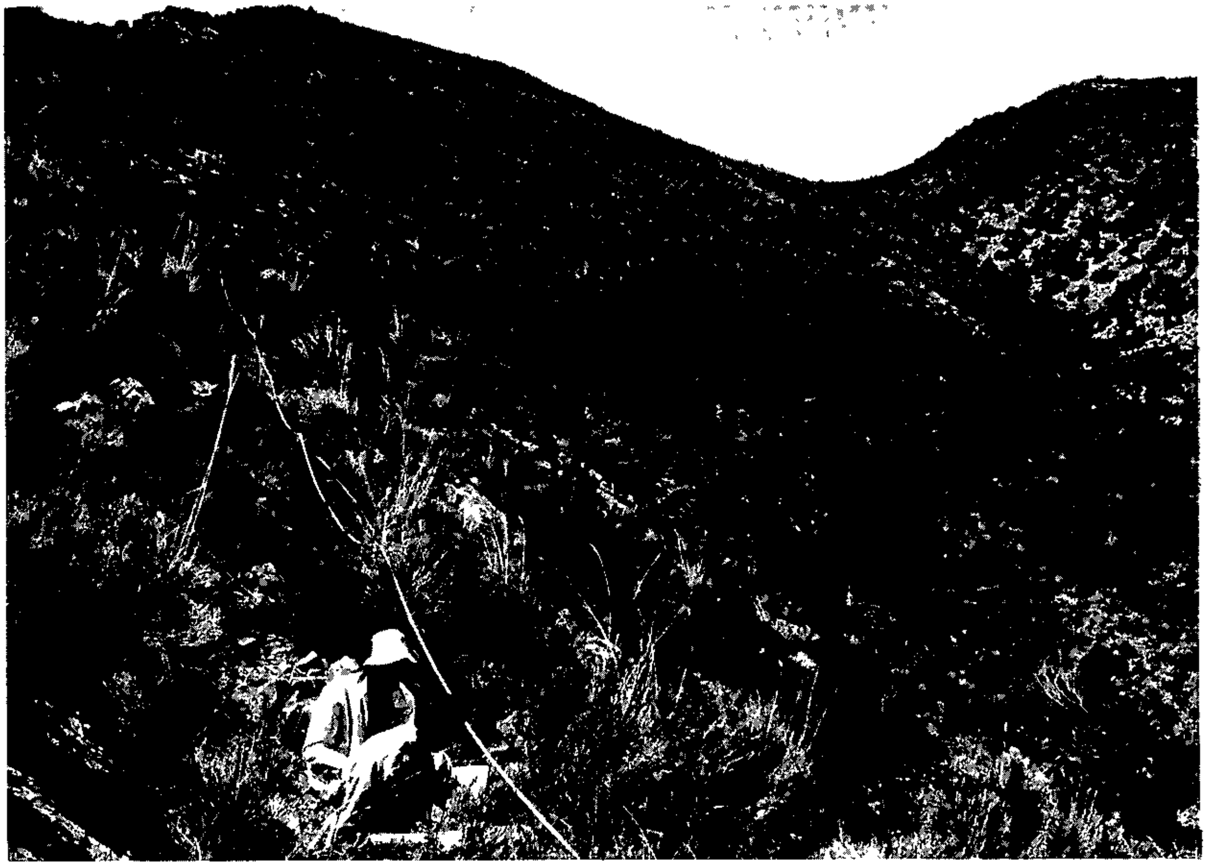

Figure 7. Open mixed community of Arid Fynbos on a southerly slope near Ladismith (see Kruger 1979 for details). Elytropappus rhinocerotis is a prominent shrub, and a Merxmuellera sp and Restionaceae spp dominate the herbs. This site is at the arid end of the fynbos gradient. Note sparse succulent shrubland of Succulent Mountain Scrub (Spekboomveld - dominated by Portulacaria afra) on northerly slopes in the right distance (see Levyns 1950)

mucronata and Lebeckia cytisoides are sometimes prominent, as are succulent shrubs like Euphorbia spp.

Shrub forms which resemble those of Karoo Veld Types (Acocks 1953) are also present. These include rigid erect shrubs with small, very stiff, usually dentate leaves, with resinous surfaces (e g Relhania).

A variety of formations is found in this type. Open proteoid shrublands such as the Leucadendron pubescens communities near Citrusdal (Figure 5) are sometimes encountered, but are not widespread. More common are various communities of a mixed character (Figures 6 and 7). Open restioid herblands are widespread in parts: in the north-west, sites with deep reddish sandy soils are usually dominated by Willdenowia striata and communities are poor in species and life forms. They resemble some communities in the Coastal Fynbos (Acocks 1953).

COASTAL FYNBOS

Much of the Coastal Fynbos in the west occurs in the 200 - 300 mm yr^{-1} rainfall zone but since it is relatively luxurious (Boucher and Jarman (1977) report total cover ranging from 65 to 80%) it does not belong to Arid Fynbos as described above.

Because of its location and the often unconsolidated substrate on which it occurs, the Coastal Fynbos ecosystem is subject to more severe disturbance than are other types. Burning, overgrazing, exploitation for fire-wood and disturbance with development of resorts are said to have resulted in the extensive live dune systems of certain parts (Walsh 1968). Phillips (1931) and Taylor (1972) have described the littoral succession briefly, and Boucher (1978) adds further descriptions of strand communities, but there is no information on succession on interior dunes, although experience shows that native species easily recolonize stabilized dunes.

There is too little information in the literature to permit a proper analysis of plant communities in Coastal Fynbos. Taylor (1978) emphasizes that Mountain and Coastal Fynbos communities differ in species composition. They are structurally alike and share the same plant families, in spite of the often large differences in physical environment. Thus the descriptions of Mountain Fynbos life-forms must serve also for Coastal Fynbos communities until further data are available. Accounts of Coastal Fynbos communities are given by Muir (1929), Taylor (1969, 1972, 1978), Van der Merwe (1976) and Boucher (1978). The present account is based mainly on Kruger (1979).

Taylor (1978) noted that two major subdivisions could be recognized within the Coastal Fynbos on biogeographic grounds; these are the fynbos on marine sands of the west coast from the Cape Flats to Elands Bay, and that on the limestones from Danger Point eastwards towards Mossel Bay. The former is ericoid and open with Restionaceae in lower strata while the latter has an upper proteoid stratum with ericoids and Restionaceae below; both types have more grass species and annuals than does Mountain Fynbos. Acocks (1953) recognised a third type, ie a dwarf fynbos of the flats on Bokkeveld Shales near Elim, but this will not be discussed here for lack of information.

Coastal Fynbos on limestones

Judging from a classification and description by Van der Merwe (1976), tall open-heath communities dominated by proteoid shrubs such as Leucadendron meridianum (eg Figure 8) appear to be representative of communities on the eastern limestones. Structurally, these communities are like any other tall open-heath of the Mountain Fynbos and include some species such as Erica plukeneti and Hypodiscus striatus, which are typical of the latter vegetation, together with strictly Coastal Fynbos species such as Protea obtusifolia, Chascanum cernuum, Thamnochortus fraternus and various species of Erica.

Figure 8. Tall open-heath of Coastal Fynbos on limestone hills near Bredasdorp. Dominant shrub is Leucadendron meridianum (see Kruger 1979 for details)

Kruger (1979) also describes a tall open-shrubland with heath, on sand about 0,5 m deep over level calcrete east of Danger Point, which differs in composition from the predominant tall open-heath described above. On the whole, the dominant structural formations on limestones appear to be open-heaths of various forms. However, Taylor (1969) describes a dwarf-heath, the Dwarf Mixed Fynbos Sub-Association, at the Cape of Good Hope, suggesting that similar formations may be found around Bredasdorp, and reports limestone dwarf-heath on the Cape Flats (Taylor 1972). He also describes a Leucadendron coniferum broad-sclerophyllous closed-scrub, poor in species, which may occur elsewhere in the limestone foreland: Boucher (1978) describes a similar community from near Betty's Bay.

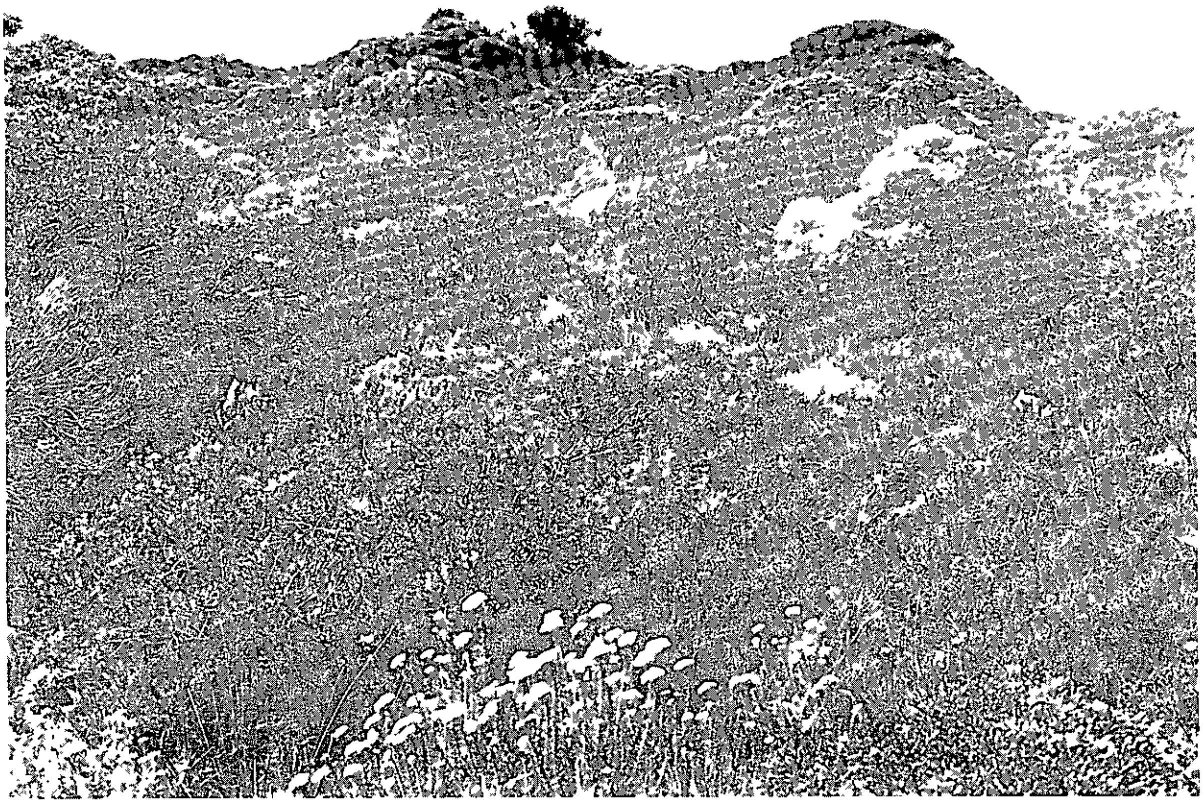

Figure 9. Mixed Coastal Fynbos vegetation on fixed coastal dunes near Betty's Bay. Prominent rounded shrubs are Leucadendron coniferum, here 2 to 3 m tall, and those with white inflorescences (eg centre foreground), are Metalasia muricata. A rhizomatous restioid herb, Restio eleocharis (discernible at the right, middle) is common in such habitats but is often the only species of this growth form. (Refer to Boucher 1978 for details)

Figure 10. Mixed community of Coastal Fynbos on relatively old drift sand at Pella, near Mamre. Note emergent broad-sclerophyllous Protea pulchra, low and mid-height narrow-sclerophylls, and tufted Restionaceae. This vegetation resembles communities of Mountain Fynbos more closely than does that illustrated in Figure 9. (Photo C Boucher)

Fynbos of coastal sands

A great variety of structural formations is encountered on coastal sands, but although descriptions are given by Taylor (1969, 1972), Boucher (1972), Boucher and Jarman (1977) and Boucher (1978), few quantitative analyses are available. Taylor (1972), in an account of the vegetation of the Cape Flats, describes structural formations which range from tall narrow-sclerophyllous closed-heath (dominated in places by Metalasia muricata and Passerina spp) to tall open graminoid-heath with Passerina vulgaris and Thamnochortus erectus, and low heaths. Communities on unconsolidated sands characteristically included a number of vigorous rhizomatous herbs such as Ehrharta villosa, and soboliferous shrubs such as Myrica cordifolia. Muir (1929), Taylor (1969) and Boucher and Jarman (1977) also describe what appears to be a typical Coastal Fynbos formation, a tall open-herbland dominated by stiff erect tufts of Thamnochortus erectus or T spicigerus, about 1,2 to 1,5 m tall. These communities are often simple in structure and poor in species.

General

Taylor (1978) discusses the biogeography of Coastal Fynbos and suggests that many of its features unique in the fynbos are due to disturbances resulting from fluctuating shorelines, and to the past influence of the then-diverted Mozambique current on the environment of the west coast. Both he and Acocks (1953) stress the tropical element of the flora, most obviously represented by low bushclumps of broad-sclerophyllous shrubs such as Euclea racemosa and Rhus lucida, and on the coast, wind-sheared clumps of stunted, sclerophyllous trees like Pterocelastrus tricuspidatus and Cassine maritima. Low forest, often dominated by Sideroxylon inerme, may be found in some sheltered localities. It is often suggested that some fynbos is seral to these scrub and forest communities, and that elsewhere Coastal Fynbos has replaced a community richer in grasses (Acocks 1953).

COASTAL RENOSTERVELD

The nature of the vegetation of the Coastal Renosterveld is poorly defined. Acocks (1953) emphasizes the rare "semi-succulent scrub", "scrub forest" and grass communities as the likely "natural vegetation" of the zone, and states: "The Rhenosterbosveld which has replaced the scrub where the soil is not cultivated, is predominantly rhenosterbos ....., with an admixture of low shrubs". Taylor (1978) and Boucher and Moll (in press) cite dominance of renosterbos, Elytropappus rhinocerotis as characteristic of the vegetation. There is some concensus on the idea that most renosterveld communities are secondary, although the agencies which deflect the vegetation from its natural condition are variable, and the true character of the potential natural vegetation is inferential.

The prevailing vegetation consists of communities in which Elytropappus rhinocerotis is dominant or at least prominent, and which are relatively rich in species. Levyns (1929b) listed 66 species in an area of 1 455 m^2 at Ida's Valley, Stellenbosch, in the western Coastal Renosterveld. Eight of these species were classified as shrubs over 0,6 m tall. Of these, one (E rhinocerotis) was an abundant evergreen cupressoid shrub, one (Metalasia stricta) a common evergreen ericoid shrub, and one (Anthospermum aethiopicum) an abundant narrow-sclerophyllous shrub. Four evergreen broad-sclerophyllous shrubs were encountered, of which Dodonaea thunbergiana was most common. Proteoid shrubs were listed as occasional. Eleven species were listed as small shrubs less than 0,6 m tall. Ericoid shrubs (eg Erica imbricata) and other narrow-sclerophylls were most important but a drought-deciduous species (Montinia caryophyllacea) was frequent, and there were a few other uncommon forms including a species of succulent shrub. The herbaceous flora consisted of 47 species, which classify as follows: one restioid, four perennial, seasonally green graminoids, two evergreen geophytes, 26 deciduous geophytes, seven annual graminoids, and seven other annual herbs. At Riversdale, in the southern Renosterveld, Levyns (1935b) found 110 species in an area of about 6 822 m^2. Aloe ferox, a succulent pachycaulous tree, emerged from the shrub canopy to form a sparse overstorey. The shrub synusia, which included about 11 species, was once more dominated by Elytropappus rhinocerotis. Narrow-sclerophyllous shrubs predominated otherwise but there were no ericoids. The few broad-sclerophylls included no proteoids. Low shrubs and herbs comprised a rich flora, but were of low proportional abundance. Levyns compiled her list in November and consequently could not identify annuals or all geophytes, but the overall impression of the herbaceous life-forms matches that of the Ida's Valley community.

These data, together with those of Taylor (1978) and Boucher and Moll (in press), permit a general sketch of the community structure of the renosterveld. Trees, either broad-sclerophylls or succulent pachycauls, are normally sparse or absent. The principal shrub stratum is dominated by much-branched cupressoid or narrow-sclerophyllous shrubs forming a nearly continuous layer 1,0 to 1,5 m tall, from which occasional broad-sclerophyllous or drought-deciduous shrubs emerge (see Figure 11).

Figure 11. Coastal Renosterveld community on lower slopes of Paardeberg, north-west of Paarl. The dominant shrub is Elytropappus rhinocerotis (Photo C Boucher)

Beneath this is a herb stratum in which seasonally green tufted graminoids predominate and deciduous geophytes and annuals seasonally are prominent. Exotic annuals such as Briza maxima, B minor and Vulpia bromoides are often common among these.

Boucher and Moll (in press) review briefly the available information on the formation types of renosterveld. With accounts of Acocks (1953) and Taylor (1978), we have a broad picture of an ecosystem in which low shrublands predominate, but with shrubby grasslands in places and spiny evergreen open-shrubland or scrub in others. Most authors agree that there are complex successional relations between the different formation categories, and suggest that the small areas of natural or near-natural vegetation in an otherwise agricultural landscape are the product of less destructive biotic influences.

STRANDVELD

The vegetation of the Strandveld " .... comprises chiefly the broad-sclerophyll woody scrub of dunes near the coast, but because of the complex interplay of fynbos and forest elements in the succession from pioneer littoral vegetation to scrub, especially along the southern coast belt, the dune succession sometimes includes an ericoid, fynbos-like scrub and sometimes proceeds from pioneer vegetation to a typical Coastal Fynbos that forms a fairly stable sub-climax" (Taylor 1978). Communities in this loose category are mapped only along the west coast but do in fact occur along the south coast as far as the mouth of the Sundays River (Acocks 1953). Taylor (1978) and Boucher and Moll (in press) provide broad descriptions of different types of community in the Strandveld.

Strand and littoral dune communities are seral and somewhat fragmentary. Colonisers along the strand include tufted graminoids such as Agropyron distichum and Eragrostis cyperoides, rhizomatous graminoids such as Erharta villosa, sprawling succulent or semi-succulent herbs and semi-shrubs such as Senecio elegans, Arctotheca populifolia, Tetragonia decumbens and Carpobrotus acinaciformis and specialised shrubs such as Myrica cordifolia and Scaevola thunbergii. Evergreen, narrow-sclerophyllous, sometimes ericoid, closed-heath develops on partly stabilized littoral dunes; Metalasia muricata and Passerina spp are typical dominant shrubs, as they are in Coastal Fynbos.

Coastal scrub communities are usually regarded as the climax of plant succession in the Strandveld. In the south, these communities are usually dominated by a few species of somewhat contorted, evergreen, broad-sclerophyllous trees, especially Sideroxylon inerme and Pterocelastrus tricuspidatus. Lower evergreen shrubs, some spiny, form an indistinct lower layer, and there is a sparse herb layer. In the west, these scrub communities tend to form low (about 1,5 m), broad-sclerophyllous, thorny thickets with a proportion of succulent and drought-deciduous shrubs. On the west coast, however, the communities are generally more open, with a diversity of life forms (e g Figure 12). Boucher and Jarman (1977) describe a variety of such communities, which range from tall open

Figure 12. Open Strandveld communities in coastal dunes on west coast, west of Mamre (Photo C Boucher)

restioid herblands, through succulent dwarf shrublands and open evergreen dwarf shrublands, to evergreen broad-sclerophyllous closed-scrub. Shrub life-forms include broad-sclerophyllous shrubs such as Rhus glauca and Pterocelastrus tricuspidatus. Some, such as Putterlickia pyracantha, are spiny, some are drought-deciduous leaf succulents (Zygophyllum morgsana and Cotyledon paniculata) or stem-succulents (Euphorbia mauretanica). Low and dwarf shrubs include evergreen narrow-sclerophyllous species (Diosma hirsuta), drought-deciduous succulents (Zygophyllum cordifolium, Mesembryanthemum crystallinum) and evergreen succulents (various species of Mesembryanthemaceae). Herbaceous and sub-ligneous climbers such as Antizoma capensis may be prominent in some situations. Restioid herbs are usually rare, although the ubiquitous Capensis species Restio cuspidatus is sometimes encountered, while tall tufted species like Thamnochortus spicigerus and Willdenowia striata may be prominent or dominant on deep sands. Seasonally green perennial graminoids such as Ehrharta calycina are prominent in many communities.

Boucher and Jarman (1977) did not present data on geophytes and annuals, but both are prominent in spring. There is a great variety of annual species, including succulents, and some open communities are dominated by annuals in the late winter and spring of years with good rainfall.

SEASONALITY

Little information about seasonality is available for plant communities in the Coastal Fynbos, Coastal Renosterveld, and Strandveld, though some observations have been recorded incidentally (Levyns 1929b, 1935b). In broad terms, seasonality in montane communities appears to parallel that of coastal communities. However, in the biome as a whole, community seasonality should be modulated by the length and intensity of summer drought. Thus, decrease in rainfall is accompanied by an increase in the relative importance of seasonally green plants and/or succulents. There is also some evidence for fynbos species responding to the east-west gradient in the proportion of winter rainfall. Williams (1972), for example, shows a marked difference in flowering phenology between species of Leucadendron from the winter rainfall zone (July to October) and those of the constant and summer rainfall zones (October to December). This account, however, refers mainly to communities in the centre of the Mountain Fynbos zone, and relies on a recent summary of information in Kruger (in press).

The phenology of fynbos communities is complex. Most species flower in spring, but a relatively large proportion of the flora in any area is in flower in any month of the year (Rycroft 1953, Van der Merwe 1966). Shrubs, however, tend to flower rather more regularly through the year than do other growth-forms. Furthermore, in shrubland communities, the flowering aspect naturally tends to reflect the seasonality of the dominant species. Because of this dominance, many communities have their period of maximum flower production in winter and early spring, though some communities dominated by Ericaceae have maximum flower production in summer. Many areas dominated by winter-flowering Protea species have their highest biomass of birds (and possibly of adult arthropods) at that time.

Summer growth rhythms among fynbos shrub species are often emphasized e g

Levyns (1964) and Taylor (1978), but Kruger's (in press) information suggests that the situation is more complicated; common dominant shrub species such as Protea neriifolia and P repens produce shoots in spring to early summer. Leucospermum tottum shows a summer rhythm and Protea arborea a bimodal, spring and autumn rhythm. Herbaceous species apparently show an even more complex pattern, and season of growth varies with species, so that one or more may be found growing actively at any time from autumn through to early summer. Thus to some degree the seasonal activities of fynbos plant communities appear to be out of phase with present climate. There is considerable asynchrony among species, with some measure of correlation among seasonalities of species of similar growth form. For example, low herbaceous species grow early in the wet season, whereas tall shrubs grow later into the dry season; there are many intermediates. Even in the case of drought-avoidance there is little synchrony. Although most shrubs shed leaves in late summer and early autumn, low shrubs and herbs may shed leaves or become dormant at any time from late spring through to late summer (Kruger in press).

PLANT SUCCESSION

Here the description of plant succession is confined to an account of community change following fire (mainly following Kruger 1977b), since this is the most common type of succession observed in the Fynbos Biome.

Field observations and information in Michell (1922), Levyns (1929b) Adamson (1935), Wicht (1948), Martin (1966), Taylor (1969) and Kruger (1977a, 1977b) indicate that most fynbos communities follow essentially similar courses of succession, as outlined below.

Immediate post-fire phase

Since hemicryptophytes are important in most communities, initial recovery is rapid. Regeneration and germination of seeds occurs for all or most species within the first 12 months after fire. Sprouting species appear within days or weeks and some are able to flower and set seed in this period. Fire-lilies and related forms

(Cyrtanthus spp, Haemanthus canaliculatus, some Orchidaceae), and almost all annuals, reproduce only in this interval.

Youth phase (up to 4 to 5 years)

Fynbos is quickly dominated by graminoid herbs and sprouting shrubs, the herbs reaching maximal above-ground biomass of up to 8 000 kg ha^{-1} after the first three to four years. In this period, canopy cover reaches about 80% of pre-burn levels. The remaining sprouting species attain reproductive maturity, while opportunistic shrubs, including succulents, mature and die. Longer-lived shrubs begin to emerge from the canopy. The vegetation becomes inflammable at about four years (Kruger 1977a).

Transitional phase (up to about 10 years)

All remaining immature plant species attain reproductive maturity in this phase. Tall shrubs emerge from the canopy and adopt the ascending branch habit.

Mature phase (up to 30 years)

Tall shrubs attain maximal height and flowering activity and full, rounded form. Reseeding low shrubs such as Erica spp begin to die; litter accumulates and lower herbaceous strata are reduced in importance; little or virtually no germination occurs.

Senescent phase

Mortality among seed-regenerating shrubs accelerates. Foliage on survivors is reduced to tufts at tips of branches, and crowns become open. With the opening of the canopy, some seed regeneration may occur. Litter and dead shoots continue to accumulate. On certain limited sites that are fertile and have moist soils, immigration of forest precursors may occur.

Thus, post-fire succession in most fynbos communities is notable for rapid initial recovery, due mainly to the growth of perennial graminoid herbs. Although germination after fire may be delayed in some instances, such as in certain species of Erica (Adamson 1935), species richness in the plant community is maximal in the immediate post-fire phase and soon after. Dominance concentration, perhaps initially intermediate, falls in the late youth phase when plants are roughly equal in height and increases to a maximum in the mature phase.

Development of fynbos communities after fire may vary considerably with vegetation structure and environmental factors. For example, Levyns (1935b) described an unusual succession in transitional sclerophyllous scrub where each of the first three years saw dominance by one or a few different reseeding species, which later declined; a germinative species of Aspalathus dominated in the fifth year, but this gradually declined, to be replaced by Elytropappus rhinocerotis, a longer-lived shrub.

ADAPTIVE RESPONSES

The plants in their present environment should have morphological and functional features which enhance reproduction and survival, specifically in the face of low concentrations of mineral nutrients, summer droughts, fire and a range of less universal stresses such as those of the sub-alpine environment. Furthermore, some adaptations should reflect the synergistic selective force of two or more of the variables listed above. Finally, the large numbers of species found in nearly all communities should be reflected in a uniquely diverse range of responses.

Cody and Mooney (1978), comparing communities from all but one mediterranean type environment (the Australian) were able to conclude: "The array of plant strategy types found in the four matched study regions is generally comparable: evergreen shrubs and trees possessing leaves of high specific weight predominate. The adaptive relationships of the leaf features to plant carbon, nutrient, and water balance in the mediterranean climatic type has been demonstrated to varying degrees. In particular, carbon balance models successfully predict the relationship of evergreenness or deciduousness to climate." Fynbos communities have several anomalous features, including differences in seasonality of growth, relatively greater diversity of leaf forms and a more complex structure. Leaves are more sclerophyllous, and have lower concentrations of nitrogen and phosphorus, at least in Mountain Fynbos. Responses of plants to low nutrient concentrations may therefore be similar to those postulated for Australian species, including special root forms (e g proteoid roots); symbiosis and/or mutualism in the rhizosphere; uptake, translocation and storage features linked to seasonal release of nutrients in the litter layer (including storage of phosphorus as polyphosphate); conservative internal nutrient balances only possible in evergreens and favoured by increased leaf longevity (see Specht 1975). Lewis and Stock (1978) have recently indicated that specialised physiological adaptations are likely to be important. Cowling and Campbell (in press) postulate that fynbos forms are adapted to nutrient stress rather than to climate and that the degree of convergence with Mediterranean and New World analogues is limited accordingly.

Adaptive responses to water regimes and to nutrients are closely interrelated and limit the range of plant forms, but Walter and Van Staden (1965) suggest that, within the evergreen shrub form, there may be fundamental differences in response, partly accounted for by rooting depth. Thus they suggest that there are "hydrostable", "hydrolabile", and intermediate species, using curves showing the seasonal course of leaf moisture content and of osmotic value for different species to illustrate the point.

The anomalous summer growth found in fynbos is sometimes ascribed to evolution of the flora in a tropical or sub-tropical palaeoenvironment, but Cody and Mooney (1978) put forward two alternative hypotheses which may be explicitly formulated as follows: first, that the small amounts of predictable summer rain in the Cape, absent in most other mediterranean climate areas, permit prolonged growth seasons, and second, that the plant responses to low nutrients dictate delayed growth.

Various authors have described means by which fynbos plants survive fire (Wicht 1945, Martin 1966, Van der Merwe 1966, Taylor 1978). These include geophytism, resprouting from subterranean buds and from dormant buds in stems. In much of the flora, survival of species is possible only through reproduction by seed. In many cases these mechanisms are not necessarily adaptive but preadaptive with respect to fire. Many species, however, do exhibit features of their life-cycles which indicate adaptations to the fire regime and Kruger (1977b) describes examples. These include the so-called "fire-lilies", other geophytes such as

Watsonia pyramidata, and various shrub forms. Levyns (1956 and earlier papers) describes features of the life-cycle of Elytroppapus rhinocerotis which fit it remarkably well to an environment with recurrent disturbance through fire. Jordaan (1949, 1965) was the first South African to show that plant species are not adapted to fire per se, but rather to a particular fire regime; adaptations are reflected in, at least, characteristic reproduction phenology, juvenile periods, and other demographic features.

Marloth (1902) has pointed to the incidence of alpine plant forms on peaks with elevations up to about 2 000 m. Although there is no consistently recognizable sub-alpine zone in fynbos vegetation, various adaptations to exposed montane situations may be expected. Kruger (in prep) has analysed vegetation developing after a rare fire at 1 800 m in the Cedarberg, and showed that the post-burn vegetation was dominated by alpine sedge forms with occasional dwarf, rosette or cushion shrubs, whereas the adjoining unburnt vegetation was dominated by typical fynbos forms of the ericoid-restioid zone with few or no alpine forms. He suggested that since many fynbos forms are clearly well adapted to current sub-alpine environments, slower-growing alpine forms are the product of more severe palaeoclimates surviving only in rare micro-habitats or the temporarily favourable post-burn environment.

Community responses to environment are poorly understood and yet no doubt provide a key to understanding the maintenance of species diversity in fynbos. Kruger (1977b) has suggested that plant succession after fire in some measure reflects niche differentiation, in that plant species share the resources of the habitat over successional time, thus avoiding direct competition. It has been suggested by Mooney (1977) that another means by which species partition resources in mediterranean type communities is through asynchronous seasonality. Thus, herbaceous plants, being shallow-rooted, grow in early spring in California and Chile and complete their annual cycles rapidly, before the surface layers are dry; shrubs tap moisture deeper in the soil and grow later. Miller and Mooney (1974) point also to the seasonal course of air temperature near the ground, which must interact with the temperature-dependent photosynthetic features of different plant forms to determine time of growth. In effect, herbs with low temperature optima are obliged to grow earlier because temperatures near ground level rise sooner. It is likely, especially in view of the complex seasonality in fynbos plant communities, that the way in which these communities are maintained must also be sought through an understanding of phenological responses to environment.

The role of plant-animal interactions in the evolution of fynbos floras is poorly understood. Rourke and Wiens (1977) and Wiens and Rourke (1978) have documented pollination by ground-dwelling rodents of certain members of the Proteaceae. These are low and dwarf shrubs, with cryptic inflorescences born at or near ground level that produce copious flows of nectar with exceptionally high sugar concentrations: these traits, they suggest, may have evolved partly in response to fire but are clear alternatives to the traits present in bird-pollinated species. Co-evolutionary relationships may yet provide a particularly profitable field for research in fynbos ecology, since the evolution of a uniquely rich flora can be ascribed only in part to geographic speciation on the lines described by Goldblatt (1978) and earlier authors.

REFERENCES

Acocks J P H 1953. Veld types of South Africa. Memoirs of the Botanical Survey of South Africa 18, 1-192.

Adamson R S 1935. The plant communities of Table Mountain. III. A six years' study of regeneration after burning. Journal of Ecology 23, 52-55.

Adamson R S 1938a. The vegetation of South Africa. British Empire Vegetation Committee, London.

Adamson R S 1938b. Notes on the vegetation of the Kamiesberg. Memoirs of the Botanical Survey of South Africa 18, 1-25.

Andrag R H 1977. Studies in die Sederberge oor (i) die status van die Clanwilliam seder (*Widdringtonia cedarbergensis* Marsh) (ii) buitelugontspanning. M Sc thesis, University of Stellenbosch.

Boucher C 1972. The vegetation of the Cape Hangklip area. M Sc thesis, University of Cape Town.

Boucher C 1978. Cape Hangklip area. II. The vegetation. Bothalia 12, 455-497.

Boucher C and M L Jarman 1977. The vegetation of the Langebaan area. Transactions of the Royal Society of South Africa 42, 241-272.

Boucher C and E J Moll (in press). South African mediterranean shrublands. Ecosystems of the world. Vol 11. Mediterranean shrublands. R L Specht (ed). Elsevier, Amsterdam.

Cody M L and H A Mooney 1978. Convergence versus nonconvergence in mediterranean-climate ecosystems. Annual Review of Ecology and Systematics 9, 265-322.

Cowling R and B Campbell (in press). Convergence in vegetation structure in the mediterranean communities of California, Chile and South Africa.

Goldblatt P 1978. An analysis of the flora of southern Africa : its characteristics, relationships and origins. Annals of the Missouri Botanical Garden 65, 369-436

Hubbard C S 1937. Observation on the distribution and rate of growth of Clanwilliam cedar, Widdringtonia juniperoides Endl. South African Journal of Science 33, 572-586

Jessop J P and A Jacot Guillarmod 1969. The vegetation of the Thomas Baines Nature Reserve. South African Journal of Botany 35, 367-392.

Jordaan P G 1949. Aantekeninge oor die voortplanting en brandperiodes vir Protea mellifera Thunb. South African Journal of Botany 15, 121-125.

Jordaan P G 1965. Die invloed van 'n winterbrand op die voortplanting van vier soorte van die Proteaceae. Tydskrif vir Natuurwetenskappe 5, 27-31.

Kruger F J 1972. Jakkalsrivier catchment experiment: investigation of the effects of spring and autumn burns on vegetation. Progress Report Project 116/25, Jonkershoek Forest Research Station.

Kruger F J 1974. The physiography and plant communities of Jakkalsrivier catchment. M Sc thesis, University of Stellenbosch.

Kruger F J 1977a. A preliminary account of aerial plant biomass in fynbos communities of the mediterranean type climate zone of the Cape Province. Bothalia 12, 301-307.

Kruger F J 1977b. Ecology of Cape Fynbos in relation to fire. Proceedings of the Symposium on Environmental Consequences of Fire and Fuel Management in Mediterranean Ecosystems. USDA Forest Service. General Technical Report WO-3. pp 230-244.

Kruger F J (1979). South African heathlands. Heathlands and related shrublands of the world, A. Descriptive studies. R L Specht (ed). Elsevier, Amsterdam. pp 19-80.

Kruger F J (in press). Seasonal growth and flowering rhythms : South African heathlands. Heathlands and related shrublands of the world, B. R L Specht (ed). Elsevier, Amsterdam.

Levyns M R 1929a. A preliminary note on the rhenoster bush and the germination of its seed. Transactions of the Royal Society of South Africa 14, 383-388.

Levyns M R 1929b. Veld-burning experiments at Ida's Valley, Stellenbosch. Transactions of the Royal Society of South Africa 17, 61-92.

Levyns M R 1935a. Germination in some South African seeds. South African Journal of Botany 1, 89-103.

Levyns M R 1935b. Veld-burning experiments at Oakdale, Riversdale. Transactions of the Royal Society of South Africa 23, 231-243.

Levyns M R 1950. The relations of the Cape and Karoo floras near Ladismith, Cape. Transactions of the Royal Society of South Africa 32, 235-246.

Levyns M R 1956. Notes on the biology and distribution of the rhenoster bush. South African Journal of Science 52, 141-143.

Levyns M R 1964. Migrations and origin of the Cape Flora. Transactions of the Royal Society of South Africa 37, 85-107.

Lewis O A M and W D Stock 1978. A preliminary study of the nitrogen nutritional status of members of the South African Proteaceae. South African Journal of Botany 44, 143-151.

Lückhoff H A 1963. Die Baviaanskloof- of Willowmore-sedar. Forestry in South Africa 3, 1-14.

Lückhoff H A 1971. The Clanwilliam cedar (Widdringtonia cedarbergensis Marsh). Journal of the Botanical Society of South Africa 57, 17-23.

Marloth R 1902. Notes on the occurrence of alpine types in the vegetation of the higher peaks of the south-western districts of Cape Colony. Transactions of the South African Philosophical Society 11, 161-168.

Martin A R H 1965. Plant ecology of the Grahamstown Nature Reserve: I. Primary communities and plant succession. South African Journal of Botany 31, 1-54.

Martin A R H 1966. The plant ecology of the Grahamstown Nature Reserve: II. Some effects of burning. South African Journal of Botany 32, 1-39.

McKenzie B, E J Moll and B M Campbell 1977. A phytosociological study of Orange Kloof, Table Mountain, South Africa. Vegetatio 34, 41-53.

Michell M R 1922. Some observations on the effects of a bush fire on the vegetation of Signal Hill. Transactions of the Royal Society of South Africa 10, 213-232.

Miller P C and H A Mooney 1974. The origin and structure of American arid-zone ecosystems. The producers: interactions between environment, form and function. Proceedings of the First International Congress of Ecology, The Hague, Sept 8 - 14, 1974. pp 38-59.

Mooney H A and D J Parsons 1973. Structure and function of the California chaparral - an example from San Dimas. Mediterranean type ecosystems. Origin and structure. F Di Castri and H A Mooney (eds). Springer Verslag, Berlin. pp 81-112.

Mooney H A 1977. Convergent evolution in Chile and California. Mediterranean climate ecosystems. Dowden, Hutchinson and Ross Inc, Stroudsburg, Pennsylvania.

Muir J 1929. The vegetation of the Riversdale area. Memoirs of the Botanical Survey of South Africa 13, 1-82.

Phillips J F V 1931. Forest-succession and ecology in the Knysna region. Memoirs of the Botanical Survey of South Africa 14, 1-327.

Pillans N S 1933. The African genera and species of Restionaceae. Transactions of the Royal Society of South Africa 16, 207-440.

Rourke J and D Wiens 1977. Convergent floral evolution in South African and Australian Proteaceae and its possible bearing on pollination by nonflying mammals. Annals of the Missouri Botanical Garden, 64, 1-17.

Rycroft H B 1953. A quantitative ecological study of the vegetation of Biesievlei, Jonkershoek. PhD thesis, University of Cape Town.

Schimper A F W 1903. Plant geography upon a physiological basis. Clarendon Press, Oxford.

Specht R L and P Rayson 1957. Dark Island Heath, Ninety-mile Plain. I Definition of the ecosystem. Australian Journal of Botany 5, 52-85.

Specht R L 1975. A heritage inverted: our flora endangered. Search 6, 472-477.

Taylor H C 1969. The vegetation of the Cape of Good Hope Nature Reserve. MSc thesis, University of Cape Town.

Taylor H C 1972. Notes on the vegetation of the Cape Flats. Bothalia 10, 637-646.

Taylor H C 1978. Capensis. Biogeography and ecology of southern Africa. M J A Werger (ed). Junk, The Hague. pp 171-229.

Van der Merwe P 1966. Die Flora van Swartboskloof, Stellenbosch en die herstel van die soorte na 'n brand. Annale Universiteit van Stellenbosch 41 serie A(14), 691-736.

Van der Merwe C V 1976. 'n Plantegroeiopname van die De Hoop Natuurresservaat. Bontebok 1(2), 1-29.

Walsh B N 1968. Some notes on the incidence and control of driftsands along the Caledon, Bredasdorp and Riversdale coastline of South Africa. Department of Forestry Bulletin 44, 1-79.

Walter H and J van Staden 1965. Über die Jahreskurven des osmotichen Wertes bei einigen Hartlaubarten des Kaplandes. South African Journal of Botany 31, 225-326.

Werger M J A, F J Kruger and H C Taylor 1972. A phytosociological study of the Cape fynbos and other vegetation at Jonkershoek, Stellenbosch. Bothalia 10, 599-614.

Wicht C L 1945. Report of the committee on the preservation of the vegetation of the South Western Cape. Special Publication of the Royal Society of South Africa, Cape Town.

Wicht C L 1948. A statistically designed experiment to test the effects of burning on a sclerophyll scrub community. I Preliminary account. Transactions of the Royal Society of South Africa 31, 479-501.

Wiens D and J Rourke 1978. Rodent pollination in southern African Protea spp. Nature 276, 71-73.

Williams I J M 1972. A revision of the genus Leucadendron. Contributions of the Bolus Herbarium 3, 1-425.

ANIMAL ECOLOGY

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INTRODUCTION

During the last two decades ecology has been transformed from a mainly descriptive endeavour into a semi-structured, predictive branch of science. The modern ecological literature incorporates powerful quantitative theories, but ecologists recognize that their science basically depends on the accumulation of data on species richness and abundance. More particularly, counts of species and their individuals in relation to time and space, and knowledge of the trophic relationships between the species, facilitate recognition of patterns in nature. Much of modern ecology is concerned with explaining variation in nature, and the identification of the evolutionary factors producing variation.

Viewed against this background, it is true to say that the ecological study of the fauna of the Fynbos Biome is still in its infancy. For instance, faunal lists are neither complete nor comprehensive; and this even applies to the relatively conspicuous, best known vertebrate classes, such as the mammals and the birds. There are large fields of ignorance in the taxonomy of the invertebrates, and virtually nothing is known about the life-histories of most of the species which have been identified satisfactorily. Thus, the accumulation of quantitative data on the distribution and abundance of at least the better known vertebrates is a prerequisite for advancing an ecological appreciation of the fauna of the fynbos.

Birds are by far the best known group of animals in the fynbos (Bigalke in press), and a start has been made in evaluating the structure and functioning of selected avian communities against the background of the paradigms of modern ecology. This endeavour was pioneered locally by Martin Cody, who studied the ways in which communities of species are assembled in response to similar selection pressures, and the role of competition in structuring communities. His approach has essentially involved comparisons between the avifaunas of four of the regions of the world with mediterranean climates (Cody 1974, Cody 1975, Cody and Mooney 1978). It should be noted that, to date, Cody's papers are the only ones in which modern ecological theory is combined with field observations of animals in the fynbos.

SPECIES DIVERSITY

This is not the place for a review of Cody's findings, but it may be of interest to paraphrase briefly some of his conclusions. Avian species richness in the fynbos is similar to that which prevails in other comparable mediterranean climate-zone biotopes. This suggests that the relatively very rich floristic composition of the fynbos is of no real, or only minor, significance as a predictor of avian species diversity, though Cody did not assess floristic richness. Perhaps the most prominent difference in species diversity and density between the avifaunas of the mediterranean regions of Chile, California, Sardinia and the south-western Cape rests in the presence in the fynbos of the Cape Sugarbird, Promerops cafer, and the Protea Seedeater, Serinus leucopterus, which are endemic specialist species tied to Protea plants, themselves without counterparts in Europe or the New World. Cody found that avian species replace one another relatively rapidly as one moves from one scrub community to another in the fynbos. The implication is that the fynbos birds, which occupy narrow niches, have become stereotyped to a narrow habitat range. In California and Chile, by contrast, the birds have broader niches and are behaviourally more plastic, allowing them, for instance, to use exotic Eucalyptus and Pinus plantations which are almost completely disregarded by birds in the south-western Cape (Bigalke in press). Finally, Cody found that the total population density of birds in comparable biotopes in Chile, California and the south-western Cape was remarkably similar, and he interpreted this as the result of similar overall productivity. Moreover, total bird density appears to be related to total insect density (Cody and Mooney 1978) and, leaving out the anomalous Cape Sugarbird, a low bird density in fynbos is related to a low insect density. These are important findings, since they point to the potential use of birds as indicators of the overall productivity of different sclerophyllous communities within the Fynbos Biome.

TROPHIC RELATIONSHIPS

This leads naturally to a consideration of trophic relationships within the Fynbos Biome. However, apart from a few qualitative statements and an assortment of unrelated empirical observations (reviewed by Bigalke in press), virtually nothing is known. Biomass values for vertebrates in the fynbos are apparently relatively low (Bigalke in press, pers obs), suggesting that only a small part of the primary production is taken by these animals and/or that primary production is low.

The construction and simulation of ecosystem models can facilitate elucidation of relationships between ecosystem components. A major goal of much of such mathematical modelling is an improved appreciation of the impact of consumers on primary producers, and the resultant effects involving the flux and compartmentalization of energy and matter within the total ecosystem. This strategy is likely to be inefficient in first attempts to understand aspects of the structure and functioning of the fynbos ecosystem. More particularly, the massive effort required for a comprehensive study of the role of the total consumer component, in the transfer of energy and other matter, will contribute relatively little to the current general understanding of the ecosystem, and it will add very little to the knowledge needed urgently for improving present conservation and management practices in the biome.

Animal populations fit into the functional framework of an ecosystem in many ways other than by energy flow and mineral cycling. For instance, in many ecosystems animals fill important roles as pollinators or dispersers of plants, and so contribute to natural successional processes. Knowledge of these processes in the fynbos is meagre, and research is needed which will expand current insights (Rourke and Wiens 1977, Wiens and Rourke 1978) into such functional aspects of the ecological system. To this end, specific objectives have been described (see Louw, this volume) in order to guide ecological research in the fynbos. Since the objectives lay stress on research which is to be directed towards well-defined and attainable goals with practical applications, ecological studies of the fynbos fauna are organized into three inter-related sections: faunal inventories and classification of biotic communities, applied biogeography and co-evolutionary aspects.

RESEARCH

The first section of research topics includes inventories of selected animal taxa, aimed at providing the basic quantitative data for a consideration of how species are associated and assembled into biotic communities, and the determinants of community structure. It will be recalled that with the exception of birds, virtually nothing is known about species richness and abundance of animals in the fynbos. The research strategy, proposed in the first instance as likely to yield maximum practical applicability in the shortest time, is multivariate analyses of as many animal populations and habitat features as possible in a variety of biotopes within the biome.

A number of concepts and theories developed by modern biogeography are revolutionizing the practice of nature conservation. For instance, the results of equilibrium and non-equilibrium island biogeography (Diamond 1975) are contributing to the erection of a scientifically conceptual framework, within which ecologically meaningful action can be taken for the conservation of individual species as well as whole biotic communities. Research in this section proposes to address a variety of questions including the following examples: How many nature reserves need to be created in order to preserve a complete series of the natural communities occurring in the Fynbos Biome? What is the optimum pattern of dispersion of nature reserves? What sizes and shapes should nature reserves have in order to preserve the minimum number of breeding units required to maintain a population of any species in the fynbos?

The third section of research topics will give attention to interactions between plants and animals in the fynbos. For instance, Bigalke (in press) reports that rodents can apparently consume the entire seasonal seed crop of the rare and endemic cedar Widdringtona cedarbergensis in a few weeks. Are these animals a significant factor in influencing regeneration of cedars in the fynbos? Does heavy seed-consumption by rodents reduce competition between cedar saplings and so promote their growth? What are the anti-predator strategies possessed by fynbos plants?

A second thrust of the research involving interactions between plants and animals is aimed at the identification of adaptations of mutual evolution between plants and their animal pollinators and seed-dispersers, and the ways in which the adaptations relate to competition between plants and between animals for resources. The interactions between plants and animals, be they pollinators, seed-dispersers or predators, can have far-reaching consequences for the dynamic structure of biotic communities; and thus they have implications for the management and conservation of the communities.

The foregoing account has concentrated on wild animals, but this is not intended to mean that ecological research involving domestic animals in the fynbos is any less important. Indeed, fynbos vegetation is browsed and/or grazed by domestic animals in many areas within the biome, and there is a need for scientific information which can be used to increase the efficiency of current range-management practices. Finally, this essay is not a rigid prescription for research. Instead, it aims at doing no more than setting out an introduction for the rudiments of a framework within which animal ecologists can contribute to the Fynbos Biome Project.

REFERENCES

Bigalke R C (in press). Aspects of vertebrate life in fynbos, South Africa. Ecosystems of the world. Vol 9. Heaths and related shrublands. R L Specht (ed). Elsevier, Amsterdam.

Cody M L 1974. Competition and the structure of bird communities. Princeton University Press, New Jersey. 138 pp.

Cody M L 1975. Towards a theory of continental species diversity: bird distributions over mediterranean habitat gradients. Ecology and evolution of communities. M L Cody and H A Mooney (eds). Bellknap Press, Harvard. pp 214-257.

Cody M L and H A Mooney 1978. Convergences and dissimilarities of mediterranean-climate ecosystems. Annual Review of Ecology and Systematics, 9, 265-321.

Diamond J M 1975. The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. Biological Conservation 7, 129-146.

Rourke J and D Wiens 1977. Convergent floral evolution in South African and Australian Proteaceae and its possible bearing on pollination by nonflying mammals. Annals of the Missouri Botanical Gardens 64, 1-17.

Wiens D and J Rourke 1978. Rodent pollination in southern African Protea spp. Nature 276, 71-73.

INVASIVE WEEDS

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INTRODUCTION

Invasive weeds are today a prominent feature of almost every major area of fynbos. Mainly shrubs and trees, most were introduced from other countries to meet practical needs. Some were distributed on a large scale. Many have escaped from their original plantations and spread at an alarming rate. Today they have a firm hold in the fynbos.

The worst invaders are a source of great concern. They are costly and difficult to eradicate by direct means such as clearing. Seeking more sophisticated controls has become an urgent priority and there is now great interest in introducing attacking organisms that are narrowly specific to the invaders, a method known as biological control. Invasions may be rapid, especially if there are frequent fires. Scattered outliers soon produce dense masses of seedlings that grow into virtual forests. Fynbos cannot survive this, and the great diversity of its flora becomes replaced by an impenetrable monotony.

HISTORY

The chief invasive weeds in the fynbos are listed in Table 1. They mainly came from Australia and South America, and most arrived in the Cape in the early nineteenth century. The reasons for their widespread adoption were chiefly to give fast-growing sources of firewood and drift-sand control. In spite of the richness of the fynbos flora, the early colonists were unable to find local plants to fill these roles as effectively as they wished. The drift-sands on the Cape Flats and near Port Elizabeth posed an especially vexing problem. They had for years resisted attempts at control and made travel across them hazardous and

Table 1.   The chief invasive weeds in fynbos

Names	Habit	Country of origin	Distribution in fynbos
Acacia cyclops A Cunn ex G Don : rooikrans	Thicket-forming shrub or tree to 6m, densely branched	Australia ca 1835	Throughout lowland fynbos, spreading elsewhere
A longifolia (Andr) Willd: long leaved wattle	Thicket-forming low shrub to 10 m tree	Australia 1827	In moist to dry fynbos from S W to E Cape
A mearnsii De Wild: black wattle	Thicket-forming tree to 15 m	Australia 1864	Widespread mostly along river-banks, S W to E Cape
A melanoxylon R Br: blackwood	Tree to 35 m	Australia 1848	Forests and margins S W to E Cape
A pycnantha Benth: golden wattle	Thicket-forming slender shrub or tree to 7 m	Australia ca 1892	S W Cape and near Port Elizabeth
A saligna (Labill) Wendl port jackson	Thicket-forming tree to 9 m, willowy branches	Australia ca 1833	Extensive, throughout fynbos
Albizia lophantha Benth: stinkbean	Thicket-forming tree to 6 m	Australia 1833	Moist sites from S W to E Cape
Eichhornia crassipes (Mart) Solms: water hyacinth+	Dense-growing water-plant with broad leaves	S America 1884	Scattered in S W and S E Cape
Hakea gibbosa (Sm) Cav: rock hakea+	Dense thicket-forming shrub to 4 m	Australia ca 1835	S E Cape
H sericea Schrad: silky hakea+	Dense thicket-forming shrub to 5 m, mostly 2 to 3 m	Australia ca 1835	Widespread in mountains, S W to S E Cape
H suaveolens R Br: sweet hakea+	Dense thicket-forming shrub to 6 m	Australia ca 1835	S W Cape
Hypericum perforatum L: Snt John's wort+	Erect-stemmed perennial to 1 m with creeping runners	Europe 1942	S W Cape
Leptospermum laevigatum F Muell: Australian myrtle	Densely-branched shrub to 8 m	Australia ca 1850	S W Cape along coast to Port Elizabeth
Myriophyllum aquaticum (Vell) Verdc: parrot's feather+	Dense-growing water plant with feathery leaves	S America ca 1921	S W and S E Cape
Nerium oleander L: oleander	Many-stemmed shrub to 6 m	S Europe ca 1811	Scattered sites in river valleys
Pinus pinaster Ait: cluster pine	Dense-crowned tree to 30 m	Europe 1680	Widespread in almost all areas
Sesbania punicea (Cav) Benth coffee-weed	Shrub to 4 m capable of forming dense thickets	S America ca 1950?	Becoming widespread along river valleys

The species marked + are proclaimed noxious weeds. (After Stirton 1978).

unpleasant. In the 1870's a successful method was found in which refuse, mostly manure, from the streets of Cape Town was mixed with seeds of Acacia saligna and spread over the sand. In other places, acacia seed seems to have been planted on a very large scale. In 1887 the Conservator of Forests distributed close to 1,5 million seeds of Acacia saligna and 0,2 million of A cyclops. A tradition of using these plants in sandy areas had begun. It continues to a large extent to-day, although curbs have appeared, arising from the concern voiced by conservationists.

Other invasive weeds in fynbos have had similar histories of early introduction and wide encouragement, followed by escape into the wild. Pinus pinaster, the cluster pine, remains today the best choice as a timber tree for planting on open slopes and in poorer soils in the fynbos. Early plantations helped meet the firewood and timber needs of the growing Cape Colony. A combination of high winds and winged seed caused the species to escape and spread, giving a park-like appearance to mountain slopes that may have been pleasantly familiar to the colonists from Britain and Europe. Whatever the reason, they attracted enough attention for pine seeds to be distributed on a wide and sometimes indiscriminate scale in Cape coastal mountains. The Australian hakeas with their dense, spine-leaved growth made good hedges, but being well-adapted to spreading as thicket-forming infestations after fires, became a serious menace to the fynbos. Hakea sericea, the silky hakea, is by far the most widespread invader in this group, and now infests nearly all fynbos mountain areas.

Most of the species listed in Tables 1 and 2 have outgrown any merits they may have had in the fynbos region and are almost entirely of nuisance value to the land manager. Acacia pycnantha was suggested for planting on the Cape Flats as a possible source of tannin. It later proved less successful than Acacia mearnsii in Natal. Later it saw some use as a sand-binder. Albizia lophantha seems to have been planted as an ornamental. Together with Acacia mearnsii it has spread and choked out stream-bank floras along hundreds of kilometers of water-ways in the fynbos. Hypericum perforatum, a major weed of other countries, was apparently introduced by accident in a batch of seed, and now poses a continual threat to agriculture in areas where it has become established.

In response to calls from agriculture, parliament passed Act No 42 of 1937, to provide for control of noxious weeds. Among the species proclaimed for action

Table 2. Potential invasive weeds in fynbos, already established and showing indications of spreading.

Acacia baileyana F Muell	Bailey's wattle
A dealbata Link	silver wattle
A decurrens (Wendl) Labill	green wattle
A elata A Cunn ex Benth	cedar wattle
Cytisus scoparius Link	broom
Elodea canadensis Michx	water-pest
Eucalyptus gomphocephala A DC	tuart, sandgun
E lehmannii (Preiss ex Schau) Benth	spider gum
Homalanthus populifolius Grah	Queensland poplar
Lantana camara L	tickberry
Lemna spp	duckweed
Myoporum insulare R Br	manitoka
Nicotiana glauca Grah	wild tobacco
Pennisetum clandestinum Hochst & Chiov	kikuyu
Pinus canariensis C Sm	canary pine
P halepensis Mill	Aleppo pine
P pinea L	stone pine
Pittosporum undulatum Vent	sweet pittosporum
Populus canescens (Ait) J E Smith	grey poplar
Rubus spp	bramble
Salvinia molesta Mitchell+	kariba weed
Solanum mauritianum Scop	bug-tree
Stipa trichotoma Nees+	nassella tussock

The species marked with + are proclaimed noxious weeds. (After Stirton 1978).

under the Act were the three hakeas that invade the fynbos. Others are listed in Tables 1 and 2. The application of the Act has proved difficult. Attempts to use it to compel land-owners to eradicate hakea have met with little success. It is notable that some potentially serious invaders such as Albizia lophantha and Leptospermum laevigatum are not listed as noxious weeds. Caution is exercised in proclaiming new noxious weeds where the authorities have not been able to monitor and control the species on public lands. The argument is that a precedent of State control should exist before the Act can be applied to private land-owners. The Act requires eradication of a noxious species by a private land-owner if he is served with a notice. For many land-owners this may pose insuperable problems. Infested mountain slopes may cost as much as R300 a hectare to clear, yet the actual rateable value may be no more than R5 a hectare and profits from grazing or wild-flower collecting may be equally small. This represents a most serious problem as some 40% of the Fynbos Biome is privately owned.

The response from both scientists and land-owners has been strengthening over the years. One of the earliest comments on the spread of the invaders came from Marloth (1908) who drew attention to infestations of acacia on the Cape Flats. Adamson (1938), Nel (1938) and Phillips (1938) noted the widening scale of the invasion in the fynbos. In 1943 the Royal Society of South Africa set up a committee to investigate the preservation of the plant life in the south-western Cape. The committee concluded that invasive plants were probably the greatest threat to the flora and immediate controls were recommended (Wicht 1945). Later authors reported similar findings (Taylor 1969a), and equally strong opinions were voiced at several conferences since 1961 (Anon 1974, 1977). In the late 1950's a Committee for the Control of Alien Vegetation was established. It promoted clearing in key areas and published a short booklet (Anon 1959). Local clearing efforts have been made by many public bodies and voluntary organizations. Numbers of private land-owners have made determined attempts at clearing, sometimes at great cost and in many cases largely successful in local areas.

Mammoth clearing tasks have been undertaken with great determination by the Department of Forestry. The Department controls over 40% of the fynbos, chiefly in the mountains. The policy for the management of public and private water catchments includes strictly enforced measures for the control of invasive weeds. The annual amounts spent in clearing in the Department's areas in the Cape have risen from R50 330 in 1971/2 to R101 108 in 1974/5. In 1974, 56 000 ha of fynbos on Forestry Department land were considered infested, 9 000 ha being at a high density. About 10 000 ha are being cleared and re-cleared each year and the work is to continue for a long time (Secretary for Forestry, pers comm). In 1975, the Department suspended its sales of seeds of Acacia saligna, A cyclops, A longifolia and Leptospermum laevigatum to land-owners who had been using them for a variety of purposes. The approximate numbers of seeds calculated from weights sold in 1973 were Acacia saligna, 5,2 million; A cyclops 2,6 million; and Leptospermum laevigatum, 15,2 million. The Department had for many years planted Acacia cyclops and A saligna along major sections of the south-western and southern Cape coasts, to control drift-sands. Although these species performed this task well, they have "spread inland over grazing veld and farmlands at an alarming rate, destroying all indigenous vegetation in their path, and, once established, are extremely difficult to eradicate" (Walsh 1968). In the Albertinia, Still Bay, Riversdale and Heidelberg Districts, Acacia cyclops took only 30 years to invade 41 000 ha of fynbos inland from the coast (B A Beukes in Walsh 1968). The

Department has ceased using these species, but immense infestations remain in coastal and nearby lowland areas.

Since 1960 the Department of Agricultural Technical Services has been active through its Plant Protection Research Institute in seeking biological control of invasive weeds in fynbos. In 1960 it began a programme on Hypericum perforatum and in 1962 on Hakea; in 1977 studies were under way for Acacia (Neser and Annecke 1973, Neser 1974a, Neser 1974b, Annecke and Neser 1977, Van den Berg 1977). The Department's Botanical Research Institute has made valuable contributions to the knowledge of the distribution and ecology of invasive weeds in the fynbos, both through its unit at Stellenbosch and the Economic Botany Section at its headquarters in Pretoria. The Institute, with the aid of a number of botanists from other bodies, recently compiled a definitive source-book on invasive plants in the Cape Province (Stirton 1978). The Department remains aware of the useful role that species such as Acacia cyclops have played in helping with problems like the wind erosion on the western Cape coast, but is keen to find replacements that are not potentially dangerous to fynbos (Kleingeld 1976, Boucher and Boucher 1978).

A number of aspects have come under the scrutiny of University-based research. In 1961, a short study of the introduction of alien acacias to the Cape was published (Roux 1961). This is being followed by a detailed historical analysis of the establishment of the main invasive weeds at the Cape, currently in preparation (G L Shaughnessey pers comm). For the acacias, brief studies have been made of their distribution, fixation of atmospheric nitrogen, production of toxic substances of possible ecological importance, and seed distribution and germination (Roux and Middlemiss 1963, Roux and Warren 1963, Jones, Roux and Warren 1963, Middlemiss 1963, Roux and Marais 1964). A further study on the distribution of the acacias was published in 1977 (Hall and Boucher 1977), and a detailed analysis of their phenology, ecology and population biology is in preparation (S J Milton pers comm). Schütte (1953) and Jooste (1965, 1966/67) published findings on attempting to control Hakea using weedicides. An ecological and taxonomic study of Leptospermum laevigatum is in preparation (C J Johnson pers comm). Plant and animal interactions have also seen attention: feeding by the striped field-mouse, Rhabdomys pumilio on acacia seeds (J David pers comm) and extensive attacks on the seed of Acacia cyclops by members of the bug family Alydidae (S Neser, S J Milton pers comm) have been studied as interesting developments. The local distribution and ecology of invasive weeds have been studied in the northern Cape

Peninsula (Hall 1961, McLachlan, Moll and Hall in prep), on Table Mountain (Moll and Campbell 1976) and in the Cape of Good Hope Nature Reserve (Taylor 1969b).

In 1972, a forum for the coordination of weeds research was provided by the National Programme for Environmental Sciences. Its Working Groups on Terrestrial Weeds and Poisonous Plants has met a number of times and organized national conferences in 1974 and 1977. Arising from the 1977 conference, the Weed Science Society of southern Africa was established in 1978. Local coordination in the south-western Cape has been aided by exchanges of views at meetings of the Cape Research Group on Invasive Plants which was founded in 1974. This body has been helpful in pointing out research priorities. Far-reaching developments may come from the proposal, put forward at the national conference in 1977, for a Fynbos Weeds Control Organization. Still under consideration, such a body could provide a much needed centre for coordinating the massive task of halting the invasion of weeds in the fynbos.

THE THREAT POSED BY INVASIVE WEEDS

The extent of the invasion by weeds and the reduced state of the fynbos have led to great concern. Satellite photographs show that the natural fynbos areas exist today in isolated patches and often narrow mountain corridors. The areas have long boundaries of contact with sources of invasive plants. The total area of the fynbos has been estimated to have been reduced by about 60% since the arrival of large human populations at the Cape (Hall 1978). Its area is now about the size of the Kruger National Park, but very much fragmented. About 24% of the remaining area has been estimated to carry light to heavy infestations of invasive weeds. Without effective action, the fynbos might become so suppressed by the invaders as virtually to disappear in most areas within a hundred years (Hall and Boucher 1977).

The threat of suppressing most of the fynbos is based upon several lines of evidence, some of which will need further critical review. The evidence of spread and establishment are everywhere to be seen in uncontrolled, infested areas. The study by McLachlan <u>et al</u> (in prep) shows that even in the controlled areas of the northern Cape Peninsula it has not been possible to bring about a substantial reduction of infestations among all mountain land within a period of 16 years since a previous survey (Hall 1961).

A serious aspect of the threat is posed by the seed biology of the two most widely invasive genera, Acacia and Hakea. In the hakeas, the seed is withheld in tough pods on the plant until there is a veld fire. Shortly after the fire the pods open, releasing large numbers of viable, winged seeds that may be blown considerable distances without being trapped by vegetation. This abundant release produces quick-growing thickets that rapidly over-top the fynbos. The acacias deposit large stores of hard-coated seeds in the soil, of the order of 1 500 to 8 200 m^{-2} (S J Milton pers comm). Various factors such as the effects of moles in the soil cause this seed store to be partly buried down to depths of 30 cm or more. Veld fires lead to rapid germination of abundant seeds that have accumulated in the uppermost layers of the soil, eventually giving rise to dense smothering thickets. Reports being investigated suggest that in Australian post-fire successions, Acacia saligna may reappear after absence of plants for some 160 years, from dormant seed. If this proves correct, invasions by this species and possibly the other Australian acacias at the Cape should be viewed in a much more serious light.

Outwardly, it would seem likely that the invasive plants could continue to spread, if unchecked, through most of the fynbos. However, there is the hope that being a population explosion that is in theory a non-continuing process in nature, some point may be reached where a broad range of natural controls could finally bring the invasion to a halt and even reverse it. Recent evidence indicates that the spread of hakea might have fallen off in at least one area (Boucher pers comm). Bugs of the family Alydidae indigenous to Africa have been found recently to be causing considerable damage to seeds of Acacia cyclops and to some extent A mearnsii at the Cape (S Neser, S J Milton pers comm). While these are hopeful developments, there is no doubt that controls must be continued and made as effective as possible.

The destruction in the fynbos from a variety of factors is reflected in the large number of threatened species it contains. The fynbos region forms less than 1% of the area of southern Africa and yet has 65% of its threatened species (Hall et al in press). With over 1 200 species in hazard, the fynbos is identified, on a world scale, as a major crisis site for the loss of genetic diversity with probably the greatest concentration of threatened plants of any temperate region. Of a sample of 70 critically threatened or recently extinct taxa, 23% had been threatened by acacia invasion, 8% by pines and only 2% by hakeas (Hall et al in press).

RESEARCH AND CONTROL PRIORITIES

The most promising solution to the invasive weed problem in the fynbos seems to lie in finding the balance of controls to suit each case. No one control alone may be enough. Biological controls may be needed to curb many of the invaders' powerful reproductive abilities. These may be allied with the judicious use of mechanical clearing and controlled burning. In critical areas, costly hand-weeding of seedlings and spraying of weedicides may be needed in follow-up procedures that may last many years after the initial clearing. Outliers have to be found and destroyed before they start new infestations. Public and private land alike will have to be treated so that no local sources of re-infestation remain, in a purposeful movement towards virtually weed-free zones in the fynbos. To coordinate all this, there is a high priority for a single body with wider powers than anything that exists at present. One may hope that the Fynbos Weeds Control Organization noted earlier in this paper might meet this requirement. It is interesting to see the valuable coordinating role being played by the source-book on the Cape's plant invaders that lists the latest controls for each species (Stirton 1978).

The integration of several controls into a programme requires a good knowledge of the target weed. This places a high priority on finding out details of its performance at various seasons, its ecology and its variability. Accurate mapping of infestations and outliers has to precede the planning of a control strategy. Monitoring new outbreaks and re-appearances must be a part of the follow-up phase. Once committed to a clearing programme, one should not stop mid-way: to do so allows the weeds to flourish once more, wasting previous efforts.

The reasons for the successes of each weed species may need to be understood to provide clues as to the best point in the life-cycle to choose for part of the control strategy. Although broad similarities exist within some groups such as the acacias, each species must be studied individually. Broad generalizations may help one understand why the fynbos may be susceptible to weed invasions, but these seem to give little help towards control. For example, it has been suggested that the fynbos is in a state of bio-climatic compression by aridity inland following the mainly colder and moister Pleistocene (Hall et al in press, Axelrod and Raven 1978). Vigorous resistance by the fynbos may be less likely in a time of climatic constraint and with high levels of local species-richness. Another view is that most invaders are much less attacked by insects and other organisms than in their land of origin, where the strategy for survival must be abundant seeding or fast growth. Free of predators in the fynbos, such strategies lead to the plant becoming an invasive weed.

These factors give one three broad priorities for research: finding the distribution of the invaders, studying their autecology and phenology, and seeking the best mixture of control measures for each case. A fourth priority, taxonomy, must not be neglected. Taxonomy at the Cape poses peculiar problems. A single mountain may carry over a thousand plant species, some highly localised. A threatened habitat near Mamre on the coastal plain has slightly more than 500 species of which 28 are variously threatened or critically rare (E Esterhuysen pers comm; Hall et al in press). Keeping natural balances in such rich communities during drastic treatments to remove plant invaders requires good taxonomic recognition systems, as does restoring formerly infested fynbos. Identification systems are incomplete or out of date except for well-worked areas such as the Cape Peninsula. Even the invaders' taxonomy needs strengthening. The widespread Acacia saligna and Hakea sericea were for a long time known by the incorrect names A cyanophylla and H tenuifolia. For effective biological control, taxonomic studies at the level of strain and variety are needed to assist entomologists seeking strain-specific insects in the invaders' lands of origin.

Finally, it is important to try to understand what might be the long-term future of the plant invaders in the fynbos. To eliminate them altogether may be impossible and other species may appear as weeds in the future. Perhaps biological control, either by indigenous or imported insects and other organisms, offers the best really long-term solution (Annecke and Neser 1977). Considerable success has been achieved at the Cape in controlling Hypericum perforatum by this means. The control of hakea by biological methods is currently showing great promise, although there have been delays caused by veld fires and by difficulties in finding and breeding the right strains of insect. This project has lasted about 17 years, costing perhaps R150 000. Against this figure, each year clearing and burning costs at least R250 000 for hakea eradication programmes by State and private groups together. Biological control may be the most cost-effective method for the future if the present crisis of massive infestations needing several controls together can be surpassed. If the biological controls can be aimed at the weeds' reproductive systems, the so-called 'useful weeds' can remain in cultivated areas without the risk of spreading into the fynbos. Alternatively, it has been suggested that artificially sterilised strains of the useful weed be created for use by vegetative propagation after the fertile form has been eradicated (Boucher and Boucher 1978). In this way, acacias might still be used for drift-sand control in coastal areas, for which they are undeniably efficient. It is clearly an important priority to find non-aggressive replacements for some of the invaders in the fynbos. With biological controls efficiently operating in the longer term, one might certainly tolerate comparatively trivial numbers of alien species in the fynbos. They need not pose the threat to the future of the fynbos which they now do, nor need they interfere with the efficiency of the fynbos areas for collecting vitally needed run-off water to feed dams essential for urban and farmland development. A high premium will be placed on water catchments with future increased human populations, and it has been shown that careful management of the fynbos can minimise water-losses by evapo-transpiration (Van der Zel and Kruger 1974). Research is needed on the effects of invasive weeds in catchments (Taylor 1974).

CONCLUSIONS

Early enthusiasm for bringing plants from other countries to the Cape and encouraging their spread had been followed by neglect when they invaded fynbos vegetation. This has caused a virtual pollution of the fynbos by invasive weeds. The reaction to warnings on the threat that this posed to the fynbos was at first small. Today, there is mounting concern to see that the invaders are suppressed. A source-book about them with advice on control measures has appeared (Stirton 1978). There has been a rapid increase recently in the amount of work being done on them in the areas of research and control on State land. Infestations on private land remain a serious problem, especially where economic incentives are weak or even strongly negative. Long-term controls may be best based on attacking organisms. Replacements may be needed that are non-invasive, for the weeds that have acquired practical uses such as sand-binding. A further practical aspect may be to avoid interference by the invaders with water catchments that are critical for meeting human needs in the region. The fynbos has about two-thirds of the threatened plants of southern Africa within its relatively small areas. Many of these species are endangered by the alien invasive weeds. At stake is the survival of major parts of the fynbos, which is on its own one of the six great floras of the world. Proper care of this heritage of plants must involve better control of invasive weeds than at present.

REFERENCES

Adamson R S 1938. The vegetation of South Africa. British Empire Vegetation Committee, London. 235 pp.

Annecke D P and S Neser 1977. On the biological control of some Cape pest plants. Proceedings of the Second National Weeds Conference of South Africa. Balkema, Cape Town. pp 303-319.

Anonymous 1959. The green cancers of South Africa. The Control of Alien Vegetation Committee, Kirstenbosch, Cape Town. 18 pp.

Anonymous 1974. Papers presented at the First National Weeds Conference 13-14 August, 1974. National Programme for Environmental Sciences, Pretoria. 214 pp.

Anonymous 1977. Proceedings of the Second National Weeds Conference of South Africa, Stellenbosch 2-4 February 1977. Balkema, Cape Town. 344 pp.

Axelrod D I and P H Raven 1978. Late Cretaceous and Tertiary vegetation history of Africa. Biogeography and ecology of southern Africa. M J A Werger (ed). Junk, The Hague.

Boucher C and D A Boucher 1978. Uitheemse indringerplante bedreig die Kaapse weskus. Elsenburg Joernaal 2, 1-11.

Hall A V 1961. Distribution studies of introduced trees and shrubs on the Cape Peninsula. South African Journal of Botany 27, 101-110.

Hall A V 1978. Endangered species in a rising tide of human population growth. Transactions of the Royal Society of South Africa 43, 37-49.

Hall A V, B de Winter, M de Winter and S A M van Oosterhout (in press). Threatened and critically rare plants of southern Africa. South African National Scientific Programmes Report. CSIR, Pretoria.

Hall A V and C Boucher 1977. The threat posed by alien weeds to the Cape flora. Proceedings of the Second National Weeds Conference of South Africa. Balkema, Cape Town. pp 35-45.

Henderson M and J G Anderson 1966. Common weeds in South Africa. Memoirs of the Botanical Survey of South Africa 37, 1-440.

Jones R M 1963. Preliminary studies of the germination of seed of Acacia cyclops and A cyanophylla. South African Journal of Science 59, 296-298

Jones R M, E R Roux and J M Warren 1963. The production of toxic substances by Acacia cyclops and A cyanophylla and their possible ecological significance. South African Journal of Science 59, 295-296.

Jooste J vd W 1965. Experiments on the control of Acacia mearnsii De Wild. South African Journal of Agricultural Science 8, 1165-1166.

Jooste J vd W 1966/67. Die bestryding van Hakea. Tydskrift vir Natuurwetenskap 6/7, 315-318.

Kleingeld I H 1976. Winderosie. Winter Rainfall Region Reports, Department of Agricultural Technical Services 3(5), 1-10.

Marloth R 1908. Das Kapland. Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition 2(3). K Chun. Gustav Fisher, Jena.

McLachlan D, E J Moll and A V Hall (in prep). A re-survey of the alien vegetation in the Cape Peninsula.

Middlemiss E 1963. The distribution of Acacia cyclops in the Cape Peninsula area by birds and other animals. South African Journal of Science 59, 419-420.

Moll E J and B M Campbell 1976. The ecological status of Table Mountain. Department of Botany, University of Cape Town. pp 1-59.

Nel J C J 1938. Die Hakea-onkruid. Boerdery in Suid Afrika 13, 11-12

Neser S 1974a. The biological control of Hakea. Papers presented at the First National Weeds Conference. National Programme for Environmental Sciences, Pretoria. pp 55-57.

Neser S 1974b. The control of St John's Wort (Hypericum perforatum) in South Africa. Papers presented at the First National Weeds Conference. National Programme for Environmental Sciences, Pretoria. pp 169-173.

Neser S and D P Annecke 1973. Biological control of weeds in South Africa. Department of Agricultural Technical Services Entomological Memoir 28, 1-27.

Phillips E P 1938. The naturalized species of Hakea. Farming in South Africa 13, 424.

Roux E R 1961. History of the introduction of Australian Acacias on the Cape Flats. South African Journal of Science 60, 203-204.

Roux E R and C C G Marais 1964. Rhizobial nitrogen fixation in some South African Acacias. South African Journal of Science 60, 203-204.

Roux E R and E Middlemiss 1963. The occurrence distribution of Acacia cyanophylla and A cyclops in the Cape Province. South African Journal of Science 59, 286-294.

Roux E R and J L Warren 1963. Symbiotic nitrogen fixation in Acacia cyclops A Cunn. South African Journal of Science 59, 294-295.

Schütte K H 1953. Hakea eradication by means of new herbicides. Journal of the South African Forestry Association 23, 30-36.

Stirton C H (ed) 1978. Plant invaders: beautiful but dangerous. Cape Town, Cape Provincial Department of Nature and Environmental Conservation.

Taylor H C 1969a. Pest-plants and nature conservation in the winter rainfall region. Journal of the Botanical Society of South Africa 55, 32-38.

Taylor H C 1969b. A vegetation survey of the Cape of Good Hope Nature Reserve. MSc Thesis, University of Cape Town.

Taylor H C 1974. Weeds in the south-western Cape vegetation. Papers presented at the First National Weeds Conference 13-14 August, 1974. CSIR, Pretoria. pp 42-54.

Van den Berg M A 1977. Natural enemies of certain Acacias in Australia. Proceedings of the Second National Weed Conference of South Africa. Balkema, Cape Town. pp 75-82.

Van der Zel D W and G J Kruger 1974. Results of the multiple catchment experiments at the Jonkershoek Research Station, South Africa. II. Influence of protection of fynbos on stream discharge. Forestry in South Africa 16, 13-18.

Walsh B N 1968. Some notes on the incidence and control of driftsands along the Caledon, Bredasdorp and Riversdale coastline of South Africa. Department of Forestry Bulletin 44, 1-79.

Wicht C L 1945. Report of the Committee on the preservation of the vegetation of the South Western Cape. Cape Town, Special Publication of the Royal Society of South Africa. pp 1-56.

CONSERVATION

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INTRODUCTION

Much of the natural vegetation and associated animal life of the biome has been replaced by towns, farmlands and planted forests. Taylor (1978) shows that no more than 40 per cent remains of the area of 44 000 - 46 000 km^2 originally covered by Acocks' (1953) Veld Types 47 (Coastal Macchia), 69 (Macchia) and 70 (False Macchia). The upper limit of what remains appears to be about 18 000 km^2.

CONSERVATION STATUS

Taylor (1978) quotes recent studies which indicate that some 500 plant species occurring in the fynbos may be endangered while about 60, mostly from the southern and south-western coasts, are probably extinct. The figure of 500 species may in fact apply to a larger area than that of fynbos, while Hall (pers comm) suggests a figure of 36 extinct species. However it is clear that a number of fynbos plants are under pressure and several have been lost.

Large mammals - elephant, hippopotamus, black rhinoceros, eland, buffalo, hartebeest and large predators other than the leopard - were exterminated in the region quite soon after the arrival of European settlers. The blue-buck, Hippotragus leucophaeus, endemic to parts of the southern Cape became extinct towards the end of the eighteenth century. Only remnant populations of bontebok, Damaliscus dorcas dorcas, and Cape mountain zebra, Equus zebra zebra, have survived. Other vertebrates which are known to be rare or endangered are listed in Appendix 1. Little is known of the status of invertebrates, but a number of rare species of Lepidoptera are protected under the Cape Nature Conservation Ordinance (19 of 1974, as amended). What remains? How well are the remnants being conserved? What are the conservation problems requiring scientific solutions? In his survey of vegetation conservation in South Africa, Edwards (1974) provides statistics on the extent and degree of conservation of fynbos (Table 1).

Table 1. Conservation status of vegetation in Fynbos Biome region, according to Edwards (1974)

Veld type (Acocks 1975)		Extent	Conserved			
			State forests		Other reserves	
		(km^2)	(km^2)	(%)	(km^2)	(%)
34 Strandveld of West Coast		6 308	3,9	0,1	60,1	0,95
46 Coastal Renosterveld		14 591	76,4	0,5	49,16	0,4
47 Coastal Macchia (Coastal Fynbos)		8 379	128,1	1,5	54,22	0,6
69 Macchia	Mountain Fynbos	17 846	2 587,2	14,5	139,09	0,8
70 False Macchia		17 866	3 761,0	21,1	0,57	0,003

Judged by the percentage of the total area (as mapped by Acocks) conserved, the conservation status of Veld Type 70 is considered excellent and that of Veld Type 69 very good. These together constitute Mountain Fynbos. Reserves in fact make up a greater percentage than indicated - about 35% - if calculated on the basis of the areas of natural vegetation remaining. While the veld of the mountains is quite well catered for, conserved areas of Coastal Fynbos are very poorly represented.

Two related transitional veld types occurring within the biome, the southern portion of Strandveld (total extent of this veld type is 6 308 km^2) and Coastal Renosterveld are also confined to the lowlands. Approximately 1 per cent of the original area of each veld type is conserved. Coastal Renosterveld now covers only about 9% of its former extent, having been replaced by wheatlands (Taylor 1978). It is significant that one of the only two reptiles and amphibians considered endangered in South Africa (McLachlan 1978) is Psammobates geometricus. This tortoise, endemic to the south-western Cape, is believed to have been distributed mainly in the lowlands of the Coastal Renosterveld.

This broad picture needs more detailed examination, for Acocks' fynbos veld types are heterogeneous and the vegetation is floristically extremely diverse, with many species endemic to small areas. Kruger (1977a) suggests the recognition of biogeographic centres and zones within the veld types, each of which should be included in any system of reserves which purports to be representative. His proposals are presented in Table 2.

Table 2. Centres and zones within fynbos vegetation types where reserves should be established (according to Kruger 1977a).

Vegetation type	Biogeographic centre	Zone
Coastal Fynbos	South-western	1 West coast
		2 South coast - Elim flats
		3 South coast - limestone hills
Arid Fynbos	North-western	4 Witteberg mountain line
	Karoo Mountain	5 East
		6 West
Mountain Fynbos	North-western	7 Cedarberg
		8 Groot Winterhoek mountains
	South-western	9 Central
		10 Southern
		11 Rivierzonderend ranges
	Karoo Mountain	12 Swartberg
		13 Little Karoo "islands"
	Langeberg	14 Lemoenshoek
	Knysna	15 Outeniquas
	South-eastern	16 Kouga River drainage
		17 Tsitsikamma
		18 Winterhoek mountains
		19 Zuurberg

Mountain Fynbos is well represented on land controlled by the Department of Forestry. This land is legally well entrenched since it may not be alienated nor may boundaries be altered without parliamentary approval (Forest Act 72 of 1968; a similar degree of protection was given to National Parks when the enabling Act was passed in 1926). Theoretically some state forests now under fynbos could be afforested, although the high value placed on their role as water catchments and the acceptance of a departmental policy of nature conservation (Ackermann 1972, 1977) makes it unlikely that this will be done to any significant degree except in parts of the southern Cape (Kruger 1977a). In any event, several large areas within state forests have already been, and others are soon likely to be, specifically protected. Table 3 shows the main reserves listed by Kruger (1977a), those likely to be proclaimed appearing in parenthesis.

Table 3. Existing large reserves and those likely to be proclaimed in Mountain Fynbos (after Kruger 1977a).

Biogeographic/ecological Zone	Reserve
5	Gamka Provincial Nature Reserve +
7	Cedarberg Wilderness Area
8	(Groot Winterhoek Wilderness Area)
9	Hottentots-Holland Nature Reserve
10	(Kogelberg Forest Nature Reserve)
18	Groendal Wilderness Area
19	Zuurberg Wilderness Area

+ Represents Arid Fynbos (a type of Mountain Fynbos).

Not all zones in Mountain Fynbos are represented in these reserves, but most may be found on existing state land. The selection and proclamation of areas specifically for the preservation of various types of Mountain Fynbos is no great task. It must however be done and the formal classification of fynbos types will provide the scientific basis. Arid Fynbos and Coastal Fynbos on the other hand are not only conserved poorly or not at all, but there is little or no public land where these communities occur. The acquisition of reserves is a major priority as Kruger (1977a) and Taylor (1978) have emphasized.

For most species of animal, a network of reserves which represent all the vegetation zones listed in Table 3 would probably ensure the survival of animal populations. However, the size of the reserves is critical for species such as the leopard, which appears to move over large home ranges. Species subject to seasonal movements in response to changes in food quantity or quality such as the Cape mountain zebra or the Cape sugarbird, quoted as an example by Kruger (1977a), require reserves which include the year-round range. Here the choice of boundaries is critical. For these reasons as well as the fact that small refuges have a high ratio of vulnerable margin to area and are likely to suffer loss of species over large periods (Diamond 1975), large reserves are preferable to small ones. Kruger's proposed target of about 19 reserves, each of at least 100 to 1 000 km^2 in area, and located so as to include the zones previously discussed, must be accepted as the minimum requirement for conserving "a representative sample of the ecosystems of an extremely rich and varied landscape" (Kruger 1977a). Particular areas, some of them quite small, will be needed in addition to include viable populations of some rare plants and animals.

CONSERVATION PRACTICES AND PROBLEMS

Management of fynbos revolves around the use of fire. The vegetation appears to be fire-dependent and the climate is one in which fire occurs naturally (Kruger 1977b, Taylor 1978). Prescribed burning at intervals of about 12 years is therefore carried out by the major landowner managing Mountain Fynbos, the Department of Forestry (Wicht and Kruger 1973). This is considered to be the approximate interval necessary for all plant species to mature and produce sufficient viable seed for reproduction (Kruger 1977b). By burning compartments at different times, a mosaic results which serves to maintain a diversity of species and successional stages, while sustained water yield is ensured. Problems arise when unplanned man-caused fires disrupt the rotation. There are also a great many questions still to be answered on, for example, the most suitable season of burn and the most suitable intervals between burns in different zones and communities, burning strategies for the conservation of rare forms and valuable woody species such as the cedar Widdringtonia cedarbergensis (Andrag 1977), long-term effects on soil fertility and burning methods.

About 65% of the Mountain Fynbos occurs on private land. Some of it has been, or will be, included in catchments proclaimed in terms of the Mountain Catchment Act (Act 63 of 1970), where landuse will be prescribed by the State. Many questions on permissible forms of utilization require answers: for example, what are the short-term and long-term effects of patch burning and grazing, widely practised on farms from the Cedarberg to the southern Cape, on soils, vegetation and water yield? The flourishing wild flower industry which has become economically important in recent years (Taylor (1978) quotes as an example the export of fresh wild flowers worth almost R50 000 from Cape Town airport in three months) is based partly on flowers picked in the veld. What are the effects of this commercial exploitation, and of the burning practised in some instances specifically to "bring on" certain species for picking? Has the large-scale removal of plant material a significant influence on the nutrient status of inherently poor soils? One may speculate in a similar fashion on the effects of commercial exploitation of Buchu (Agathosma betulina, A crenulata).

It is probably true that at least most vertebrate species are enabled to survive by rotational burning which maintains a mosaic of different vegetation age classes, but very little indeed is known about the precise effects on populations. Season of burn has to date been considered entirely from the point of view of its effects on plants, while animal phenology has been neglected. There is no information on the effect of different scales of burn on animal populations. It may well be that economic considerations may dictate policies detrimental to populations of small animals with limited mobility, especially if they are limited in their distribution. Clearly there is a vast scope for research on the relationships between fynbos, animals and fire.

Invasion by pest plants is perhaps the best known problem plaguing managers of fynbos. So much has been written on this subject that it will suffice to refer to Taylor's (1978) recent overview and the chapter entitled "Invasive Weeds" in the present publication.

In contrast to plants, few exotic vertebrates have become established in fynbos. The American grey squirrel Sciurus carolinensis is common in the south-west Cape but is apparently confined to urban and agricultural environments and exotic forest plantations (Millar in prep). Himalayan tahr (Hemitragus jemlahicus) which escaped from the Groote Schuur Zoo on to Table Mountain at some time after 1935 (Bigalke 1977) are said to have numbered at least 600 by 1976 and to have been reduced to less than 200 in the course of a control programme (Hey 1978). It seems likely that the species could fare equally well elsewhere in fynbos environments and total extermination on Table Mountain appears the only real safeguard against possible escape and establishment elsewhere.

Increasing recreational use of reserves in Mountain Fynbos brings another category of problems to the fore. Research on human behaviour in wild areas, such as the pioneer study by Andrag (1977) in the Cedarberg, and on the effect of recreational use on the environment as well as on the users, will become more and more necessary if conservation and recreation are to be reconciled by scientific planning.

Finally, it should be appreciated that the study of the wild plant and animal resources of land used primarily for urban development, agriculture and forestry is an almost totally neglected field of conservation research. McLachlan (1978) points out that many reptiles and amphibians have benefited from man's activities, and the fact that some birds and a few mammals are common in gardens and other urban environments hardly needs emphasis. The ecology of farmlands and of plantations of exotic trees has however been little studied. Winterbottom (1972) describes the avifauna of farmlands and plantations in the south-western Cape. We need to know a good deal more about the effects of agricultural and forestry practices on the composition and abundance of the flora and fauna of farms and forests in order to devise means of conserving as much as possible of this land.

CONCLUSION

Conservation of the unique Fynbos Biome for the future requires an active policy of land acquisition for poorly conserved communities, the selection and proclamation of ecological reserves on public land which is already reserved, and active research on a host of problems associated with conservation management, both within reserves and on private land. When results are forthcoming, the machinery to put them into practice must be available. For this, adequate funds and manpower must be provided to control and manage conserved areas and to advise private landowners on conservation practices.

REFERENCES

Ackermann D P 1972. The proclamation of wilderness areas by the Department of Forestry. South African Journal of Forestry 82, 19-21.

Ackermann D P 1977. Nie-kommersiële aktiwiteite van die Departement van Bosbou. South African Journal of Forestry 103, 1-4.

Acocks J P H 1953. Veld types of South Africa. Memoirs of the Botanical Survey of South Africa 28.

Andrag R H 1977. Studies in die Sederberge oor (i) die status van die Clanwilliam Seder (Widdringtonia cedarbergensis Marsh) (ii) Buitelugontspanning. MSc thesis, University of Stellenbosch.

Bigalke R (Sen) 1977. The Himalayan tahr on Table Mountain. Zoologica Africana 12(2), 503.

Diamond J M 1975. The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. Biological Conservation 7, 129-146.

Edwards D 1974. Survey to determine the adequacy of existing conserved areas in relation to vegetation types. A preliminary report. Koedoe 17, 2-37.

Hey D 1978. Report on the future control and management of Table Mountain and the Southern Peninsula mountain chain. Government Printer, Pretoria.

Kruger F J 1977a. Ecological reserves in the Cape fynbos: toward a strategy for conservation. South African Journal of Science 73, 81-85.

Kruger F J 1977b. Ecology of Cape fynbos in relation to fire. Proceedings of the Symposium on Environmental Consequences of Fire and Fuel Management in Mediterranean Ecosystems. USDA Forest Service. General Technical Report WO-3. pp 230-244.

McLachlan G R 1978. South African Red Data Book - Reptiles and Amphibians. South African National Scientific Programmes Report 23. 53 pp.

Meester J A J 1976. South African Red Data Book - Small Mammals. South African National Scientific Programmes Report 11. 59 pp.

Millar J (in prep). Biology of the Grey Squirrel (Sciurus carolinensis) in the Western Cape. Thesis, University of Stellenbosch.

Siegfried W R, P G H Frost, J Cooper and A C Kemp 1976. South African Red Data Book - Aves. South African National Scientific Programmes Report 7. 108 pp.

Taylor H C 1978. Capensis. Biogeography and ecology of southern Africa. M J A Werger (ed). Junk, The Hague.

Wicht C L and F J Kruger 1973. Die ontwikkeling van bergveldbestuur in Suid-Afrika. South African Journal of Forestry 86, 1-17.

Winterbottom J M 1972. The ecological distribution of birds in southern Africa. Monographs Percy FitzPatrick Institute of African Ornithology 1, 1-82.

Appendix: Vertebrate animals of the region capensis listed in the South African Red Data Books.

Reptiles and amphibians (McLachlan 1978)

Geometric tortoise Psammobates geometricus: endangered by disappearance of lowland habitat

Rain frog Breviceps gibbosus: vulnerable due to limited distribution

Cape platanna Xenopus gilli: rare due to localised distribution

Ghost frog Heleophryne rosei: rare due to localised distribution

Micro frog Microbatrachella capensis: rare due to localised distribution

Cape dainty frog Cacosternum capense: rare due to localised distribution

Arum frog Hyperolius horstockii: rare due to localised distribution

Birds (Siegfried et al 1976)

Victorin's scrub warbler Bradypterus victorini: may be vulnerable.

Protea seed-eater Poliospiza leucoptera: rare and localised

Small mammals (Meester 1976)

Lesueur's wing-gland bat Myotis leseuri: rare, limited distribution

Cape Fat mouse Steotomys pentonyx: rare, limited distribution

Cape greater gerbil Tatera afra: rare, limited distribution

Spiny mouse Acomys subspinosus: rare, limited distribution

Verreaux's rat Praomys verreauxi: rare, limited distribution

CONCLUSIONS AND RECOMMENDATIONS

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INTRODUCTION

From the time of the earliest explorers, even the most casual visitor to the western Cape has been impressed by its natural beauty. To those of us who have been privileged to live here and experience the drama of the mountains, the splendid shoreline and the spectacularly rich flora, it means a great deal more. Perhaps our appreciation has become clouded by sentimentality and subjective aesthetic criteria while the economist, professional planner, politician and even the suburban tax-payer would demand more substantive reasons for concern over the future of the natural environment of this area.

MOTIVES FOR CONSERVATION

In the western Cape, time has long since run out for such luxuries as polemics between ecologists and economists. The Fynbos Biome, of which the south-western Cape is an integral part, has become so threatened during the past two decades that immediate action is required. For those who still require convincing, I need only draw their attention to Table Mountain - one of our national monuments. It is eroded, littered with unsightly debris, disfigured by grotesque buildings, covered with alien weeds and has become an eyesore to the layman and a tragedy to the ecologist. "A normal consequence of urban development", the economist may answer, but this would be inadequate, for even a superficial survey of the Fynbos Biome will reveal that the natural vegetation is being destroyed, in rural as well as in urban areas, by the inroads of agriculture, forestry and the uncontrolled invasion of exotic weeds. Urban sprawl, irresponsible development of holiday resorts and roadsystems as well as overgrazing and badly planned fire-regimes have all taken their toll. It is not surprising therefore that Dr Hall of the Bolus Herbarium has been able to compile such a long list of threatened and endangered plant species within this biome (this volume).

It is an easy task therefore to convince even the most obdurate that the Fynbos Biome is indeed threatened; but persuasive reasons for its conservation, other than sentimental, are less obvious. To me personally, aesthetic reasons, even though subjective, are sufficient. To those, however, who require "hard-nosed" reasoning, I can offer three important motives for preserving the natural environment of this biome. First of all, many of the still unspoilt areas within the biome are in relatively inaccessible montane regions where they act as vitally important catchment areas for water-impoundment schemes. The importance of managing and conserving these areas correctly, especially when viewed against the exponential population growth in the western Cape, requires no further elaboration. Secondly, it would be difficult to overemphasize the importance of the natural beauty of the biome in providing recreation and acting as a magnet for both national and international tourists. Finally, the biome must be considered unique from a scientific viewpoint. The incredible species diversity (over 6 000 species) and the marked degree of endemism have resulted in the biome being classified as one of the plant kingdoms of the world. This, to my mind, places us under an obligation towards the international scientific community to do everything possible to conserve this unique biota.

A PATTERN OF IGNORANCE

When assessing the major threats to the biome previously, I intentionally omitted the most important threat, namely our ignorance about the biology and ecology of this unique region. I did so as this aspect is sufficiently important to warrant special attention

Even a superficial perusal of the foregoing chapters of this document should convince the reader that, in spite of over two centuries of scientific endeavour in the western Cape, our knowledge of the ecology of this region is almost non-existent. Let as examine some of the more important issues:

1. Although various vegetation surveys of the region have been undertaken, there is as yet no clear-cut agreement on a definition of fynbos or where it begins or ends. There is therefore, a definite need for extensive surveys, mapping and structural and functional classifications.

2. Meteorological data have been collected within the margins of the biome for many years, but little or no attempt has been made to synthesize and interpret these data. Moreover, weather stations have understandably been conveniently placed near towns and homesteads. We know virtually nothing about the micro-climate of the more remote montane regions and the inter-relationships of topography, micro-climate and the biota.

3. We have a fair knowledge of the origin and distribution of soil types within the biome. An understanding of the relationships between soil type, nutrient cycling and plant ecology is almost completely lacking.

4. The floristic taxonomy of the biome is far from complete. There is also an acute shortage of competent taxonomists and plant identification services for ecologists.

5. We have only begun to scrape the surface of the palaeo-ecological history of the fynbos. Such studies are essential, however, for gaining an insight into the ecological stability of the biome in terms of its geological history, in order to complete our understanding of the functioning of the biome as a whole.

6. The profound effects of fire on the ecology of the biome are still poorly understood and research in this direction must be given very high priority.

7. Our knowledge of present and past patterns of land-usage is very meagre indeed. The future use of land within the biome for agricultural and forestry expansion will have to be rationalized against the urgent requirement for the conservation of threatened species and habitats. The effect of relatively new industries, such as the harvesting of cut flowers for export, on the vegetation, must be evaluated and if necessary controlled. Finally the impact of grazing and the attendant burning practices on the natural vegetation is very poorly understood.

8. Faunal surveys in the biome are still incomplete, particularly for the invertebrates. The ecological role of animals, for example as pollinators, in the various ecosystems is virtually a closed book.

9. Although the massive invasion of the biome by alien weeds is only too apparent, very little is known about the autecology of these species. Why are they all so successful? Which practices promote their invasion and what are the major ecological factors governing their distribution?

10. Finally our ignorance about the functioning of ecosystems within the biome is staggering. Geo-chemical cycling, water relationships, herbivory, competition, food chains and bioenergetics are all aspects which will require attention within the framework of ecosystems research.

A PLAN OF ACTION

From the foregoing discussion it should be clear that not only is the Fynbos Biome seriously threatened, but also that the problems which will have to be faced in the rational planning of future management practices in this biome are very complex indeed. There is no single organization which will be able to undertake this formidable task. It is clearly a case for a well-coordinated cooperative research programme.

Some of the problems, particularly the control and eradication of invasive weeds, and large scale research on the ecological effects of fire, are of such a magnitude that they can only be undertaken by large state departments. Similarly, expensive long-term surveys of vegetation patterns and land-usage could profitably be undertaken by the State. Nevertheless, the university departments have a vital role to play. Their expertise in computer services, remote sensing, plant physiology, soil science and ecology will be essential in gaining an understanding of the autecology of selected species and the functioning of ecosystems.

The National Programme for Environmental Sciences of the CSIR has recognized the urgent need for a cooperative programme and is to be congratulated on its efforts thus far in coordinating and launching the first phase of this programme.
The objectives of the programme have been described and motivated in detail elsewhere (A description of the Fynbos Biome Project, South African National Scientific Programme Report No 28, June 1978). No purpose will be served in restating them here. Suffice it to say that the objectives have been clearly

defined to answer many of the questions posed in this paper and that the research has been carefully phased over a period of approximately 10 years. This will ultimately provide decision-makers with a sound scientific basis for formulating a master-plan for the conservation and management of this unique biome. The success of the programme will, in my opinion, depend largely on the degree of coordination which is achieved between the various research workers and to what extent the participants are able to adapt flexibly to new directions as information becomes available. This in turn will require the highest standards of creative and disciplined leadership on the part of a senior coordinator.

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TITLES IN THIS SERIES

1. *A description of the Savanna Ecosystem Project, Nylsvley, South Africa. December 1975. 24 pp.
2. *Sensitivity analysis of a simple linear model of a savanna ecosystem at Nylsvley. W M Getz and A M Starfield. December 1975. 18 pp.
3. *Savanna Ecosystem Project - Progress report 1974/1975. S M Hirst. December 1975. 27 pp.
4. Solid wastes research in South Africa. R G Noble. June 1976. 13 pp.
5. *Bibliography on marine pollution in South Africa. D A Darracott and C E Cloete. June 1976. 131 pp.
6. *Recycling and disposal of plastics waste in South Africa. R H Nurse, N C Symington, G R de V Brooks and L J Heyl. June 1976. 35 pp.
7. South African Red Data Book - Aves. W R Siegfried, P G H Frost, J Cooper and A C Kemp. June 1976. 108 pp.
8. South African marine pollution survey report 1974-1975. C E Cloete and W D Oliff (editors). September 1976. 60 pp.
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22. Cooperative National Oceanographic Programme. SANCOR. January 1978. 19 pp.

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27. Nylsvley - A South African Savanna Ecosystem Project: objectives, organization and research programme. March 1978. 37 pp.

28. A description of the Fynbos Biome Project. June 1978. 25 pp.

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35. South African Antarctic Research Programme, 1978-1982. SASCAR. December 1978. 39 pp.

36. Aboveground biomass subdivisions in woody species of the Savanna Ecosystem Project Study Area, Nylsvley. M C Rutherford. January 1979. 33 pp.

37. Marine Line Fish Research Programme. SANCOR. April 1979. 17 pp.

38. The Southern Ocean - South African Cooperative Research Programme. SANCOR. May 1979. 26 pp.

39. The Transfer of Pollutants in Two Southern Hemispheric Oceanic Systems. Proceedings of a workshop held at Plettenberg Bay, South Africa, 23-26 April 1979. 188 pp.

40. Fynbos ecology : a preliminary synthesis. J Day, W R Siegfried, G N Louw and M L Jarman. December 1979. 166 pp.

*Out of print.