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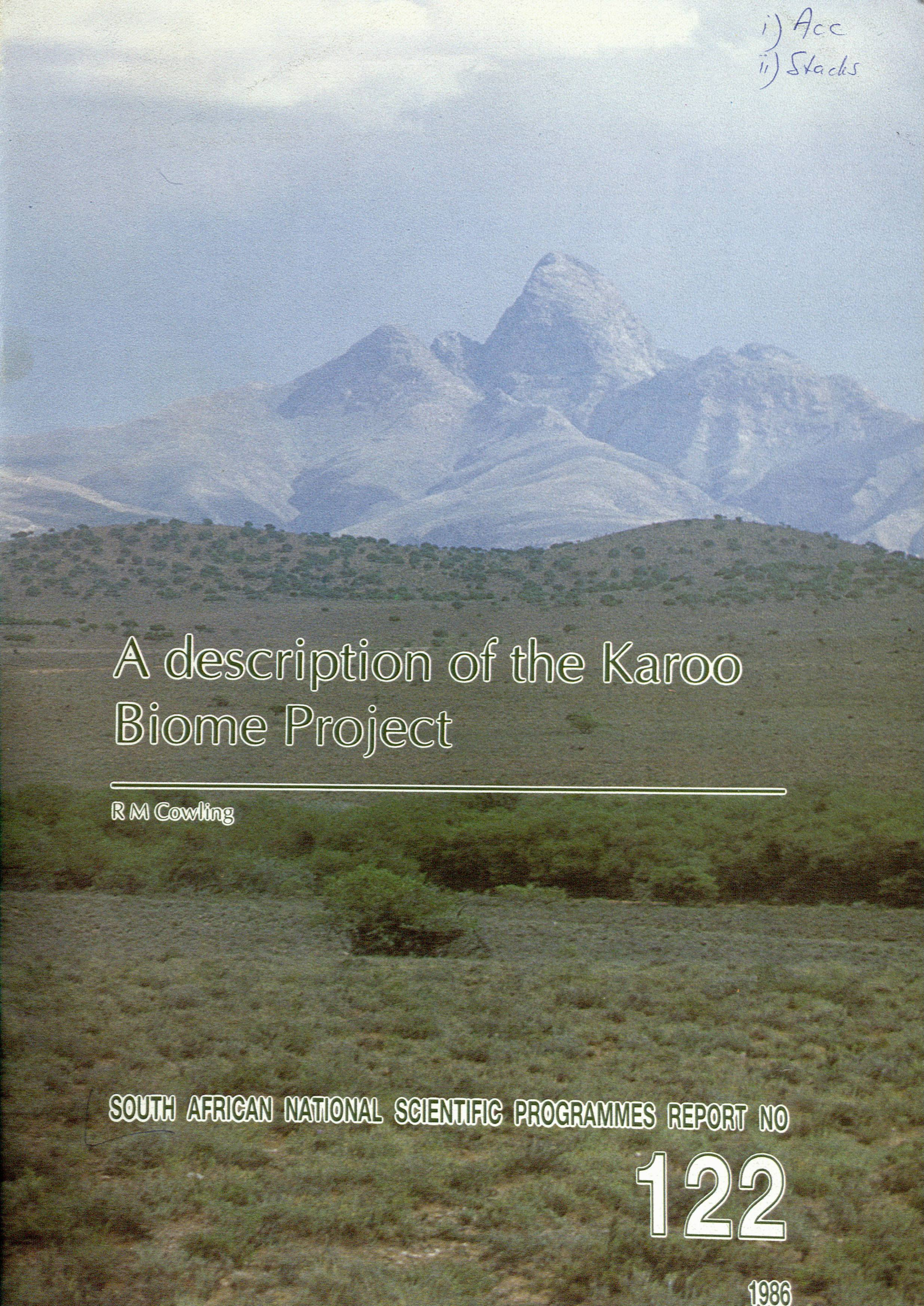

A description of the Karoo Biome Project

R M Cowling

SOUTH AFRICAN NATIONAL SCIENTIFIC PROGRAMMES REPORT NO

122

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A report of the Committee for Terrestrial Ecosystems
National Programme for Ecosystem Research

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PREFACE

The National Programme for Ecosystem Research is a cooperative undertaking of scientists and scientific institutions in South Africa concerned with research related to environmental problems. The National Programme includes research activities in inland waters and terrestrial ecosystems and deals with all aspects of nature conservation.

The Committee for Terrestrial Ecosystems has developed its programme within the five major biomes of South Africa - forest, fynbos, grassland, karoo and savanna. In each of these systems, research is designed to develop a predictive understanding of structure and functioning. The research is being coordinated within suites of both site-specific and extensive projects.

The Karoo Biome Project has recently been initiated to coordinate existing and to stimulate new research in the arid and semi-arid shrublands (karoo) of South Africa. The project will complement existing range management research by providing the structure and support for research in all aspects of karoo ecology. While most of the work to be undertaken will be financed by participating organizations, research by universities and other independent research groups will be supported by the National Committee for Ecosystem Research from funds contributed largely by the Department of Environment Affairs.

ACKNOWLEDGEMENTS

The key questions in this document were revised at a workshop held at Zuurberg during 21-22 October 1985. The workshop would not have been possible without the aid and cooperation provided by the Department of Agriculture and Water Supply, Cape Provincial Administration, Orange Free State Provincial Administration, National Parks Board and the National Botanic Gardens. Comments and discussion by workshop participants are gratefully acknowledged. In particular I thank G I H Kerley, M E Meadows, E J Moll, M C Rutherford and V R Smith for collating revised lists of key questions.

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Many thanks to C McKinnon for secretarial support in the past and to T Greyling presently.

ABSTRACT

The ecological characteristics and ecological problems of the karoo biome are briefly described. A conceptual basis and guidelines for the development of the Karoo Biome Project are outlined by addressing project goals, project structure and research strategy, relevant research fields and key questions. No attempt was made to formally phase the Project. It is hoped to stimulate research concurrently in a variety of fields and at different levels as dictated by research priorities and manpower availability. An analysis of existing research projects in relation to research fields and key questions indicates that studies are urgently required on the adaptive physiology, behaviour, and reproductive biology of selected species and growth forms in relation to various climatic and defoliation regimes. Without these data it will not be possible to develop community and ecosystem models of meaningfully accurate predictive power.

SAMEVATTING

Die ekologiese karakter en ekologiese probleme van die karoobioom word kortliks beskryf. 'n Konseptuele basis en riglyne vir die ontwikkeling van die Karoo-Bioomprojek word omlyn deur projekdoelwitte, projekstruktuur en navorsingstrategie, verbandhoudende navorsingsvelde en sleutelvrae aan te spreek. Geen poging is gemaak om die Projek to faseer nie. Dit word gekoester dat navorsing gelyktydig in 'n verskeidenheid van navorsingsvelde en op verskillende vlakke gestimuleer sal word soos gedikteer deur navorsingsprioriteite en die beskikbaarheid van mannekrag. 'n Ontleding van bestaande projekte met betrekking tot navorsingsvelde en sleutelvrae dui daarop dat studies op die adaptiewe fisiologie, gedrag, en reproduktiewe biologie van uitgesoekte spesies en groeivorms in verhouding tot verskillende klimaats- en ontblaringsregimes dringend benodig word. Sonder hierdie data sal dit nie moontlik wees om ekosisteem- en gemeenskapsmodelle met akkurate voorspellingskrag te ontwikkel nie.

TABLE OF CONTENTS

INTRODUCTION

The Karoo-Namib Region (Werger 1978; White 1983) comprises the extensive arid and semi-arid areas of the south-western part of southern Africa (Figure 1). The region encompasses a high diversity of climates, landforms, soils and vegetation. Recently Rutherford and Westfall (1986) have divided the region into three biomes on the basis of the Summer Aridity Index, percentage winter half-year rainfall, and life form mix. These biomes are: Nama-Karoo Biome, Succulent Karoo Biome and the Desert Biome (Figure 1).

While the Desert Biome is confined to the coastal forelands of Namibia and southern Angola, the Succulent Karoo and Nama-Karoo Biomes are centred in South Africa. These comprise the karoo biome (sensu Huntley 1984). The biome occupies 427 015 km^2 or 35,1% of South Africa. Vegetation is a dwarf open shrubland. The biome is used almost exclusively for extensive pastoralism and supports a profitable small stock industry. Of the total gross national income derived from small stock, 36% of the wool, 48% of the mutton, 60% of the mohair and 60% of the goat meat incomes are produced in the Karoo Region (Roux et al 1981). The area's considerable contribution to the gross domestic product of South Africa is dependent on veld as a primary source of fodder for small stock. There are thus strong economic motives for gaining a predictive understanding of the structure and functioning of karoo ecosystems.

The establishment of the Karoo Biome Project has lagged behind those for other South African biomes. Although much applied research has been undertaken by agro-ecologists (for reviews see Roux et al 1981; Roux and Vorster 1983a; Vorster and Roux 1983; Vorster et al 1983), basic research data are few and have made little impact in the open literature. The launching of the Karoo Biome Project to optimize research efforts through formal coordination within the structure of a collaborative research programme is therefore a timely development.

This document outlines the goals, project structure and research strategy, and research fields and key questions for the Karoo Biome Project. The key questions have been revised and accepted by the Project Steering Committee and the karoo research community convened at a workshop in October 1985. All current ecological research projects being undertaken within the karoo biome are listed below. New projects to be funded by the National Programme for Ecosystem Research will be evaluated in terms of their relevance to key questions listed in this document.

Background information on the ecological characteristics and environmental problems in the karoo biome is summarized below. For more extensive coverage readers are referred to Adamson (1938), Acocks (1953), Werger (1978), Roux et al (1981), Roux and Vorster (1983a), Vorster and Roux (1983), White (1983), Huntley (1984), Cowling et al (1986a), Cowling et al (1986b), and Rutherford and Westfall (1986).

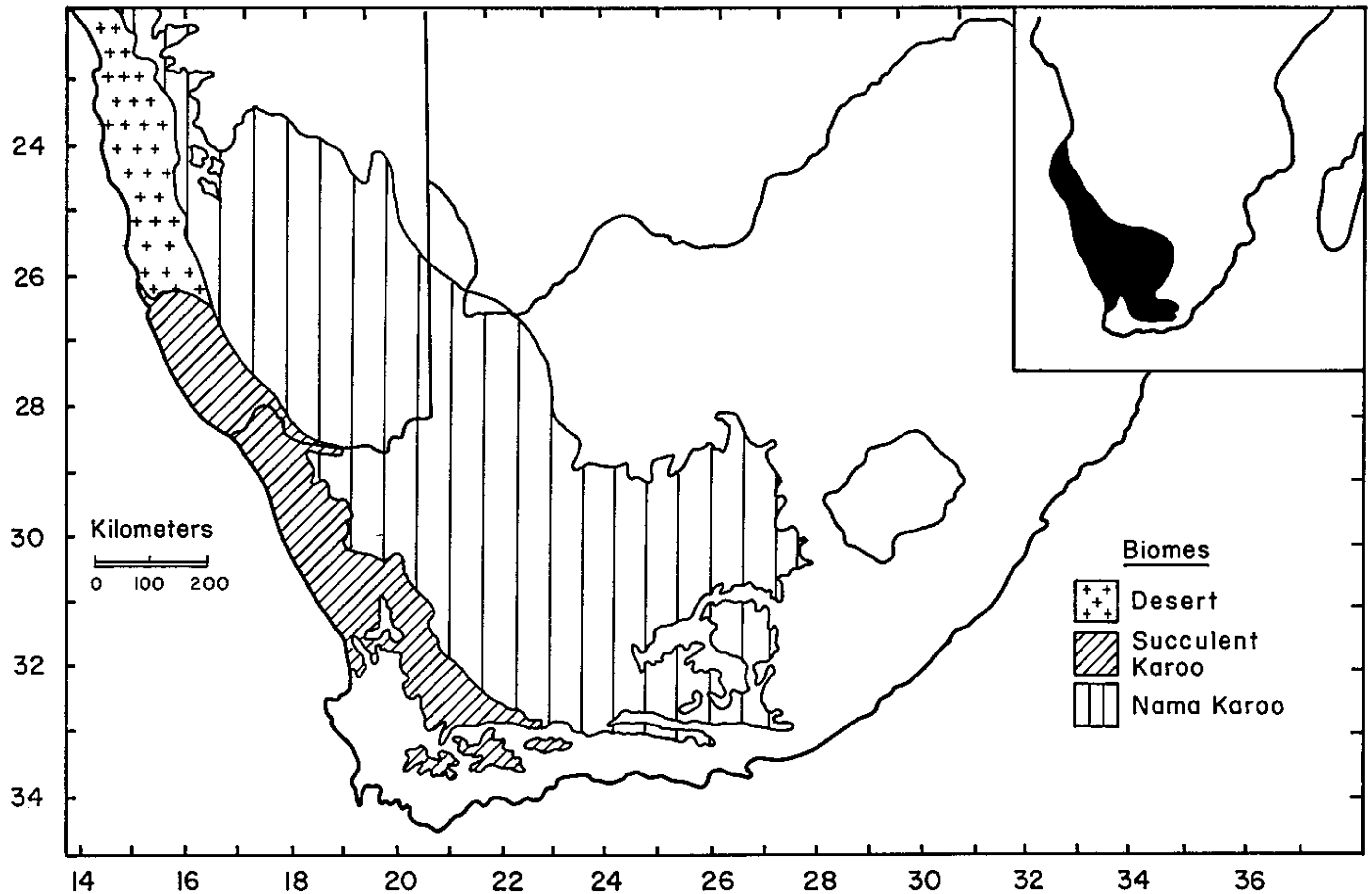

FIGURE 1. The Karoo-Namib Region in Africa (insert) and southern Africa showing the distribution of three biomes recognized by Rutherford and Westfall (1986).

ECOLOGICAL CHARACTERISTICS OF THE KAROO BIOME

GEOLOGY, PHYSIOGRAPHY AND SOILS

The geology and physiography of the area are very varied. Relatively low lying and warm areas occur seawards of the Great Escarpment. In the south these are the Great Karoo, Little Karoo and Robertson Karoo, and in the west, the Tanqua Karoo and the Namaqualand coastal belt (Figure 2). Inland of the Great Escarpment, which incorporates the Roggeveld, Nieuveld and Sneeuberg Mountains and may exceed 2 500 m, lies the vast frosty peneplain of the Upper Karoo. Other elevated regions include Bushmanland, Namaqua Highlands and the Richtersveld in the extreme west of the northern Cape.

Rocks of the Karoo Sequence predominate in the Great and Upper Karoo. Soils are weakly developed, shallow and alkaline (pH 7,0 to 8,3). Quaternary Kalahari Sands occur in the extreme north, whereas rocks of the Cape Supergroup (Bokkeveld and Witteberg Groups) cover a limited area in the south. In the north-western Cape the Karoo beds have been eroded to expose granites of the Basement complexes. Here soils are both deeper and sandier, as they are along the Namaqualand coast where there exists a fairly wide strip of Recent calcareous sand. For more details see Cowling et al (1986a).

CLIMATE

Climates of arid and semi-arid regions are usually characterized by extremes in temperature and great variability in both the amount and timing of rainfall. In this respect the climate of the karoo biome is no exception owing to its unfavourable geographic location relative to the rain-bearing circulation patterns in South Africa (Booysen and Rosswell 1983).

Schumann (1949) recognized three major climatic regions in the Karoo, characterized in terms of rainfall seasonality (Figure 2). The winter rainfall area in the western part of the biome receives more than 60% of its rain from cyclonic fronts in winter. Along the coast, dry season precipitation occurs in the form of fog. In the even rainfall area, rain may fall at any time of the year. Winter rain is associated with the deep penetration of cyclonic fronts. Cut-off low pressure cells in spring and autumn often result in heavy falls (Heydorn and Tinley 1980). Summer rain results from an extension into the region of thunderstorm activity from the north and east. Rainfall reliability is greatest in the southern and eastern parts and lowest in the northern and western parts (Anon 1957). Mean annual rainfall increases from less than 100 mm in the west to more than 400 mm in the east, but for most of the biome it rarely exceeds 250 mm (Figure 2). During winter snow is often recorded on the high altitude areas of the Great Escarpment.

Mean annual temperatures vary from 22,5° C in the north-west to 15° C on the west coast and the Great Escarpment (Schulze 1965). Greatest diel and annual temperature variation is recorded in the Upper Karoo where the incidence of frost is also high (up to 180 days per year). The low altitude areas in the south and west are relatively frost-free.

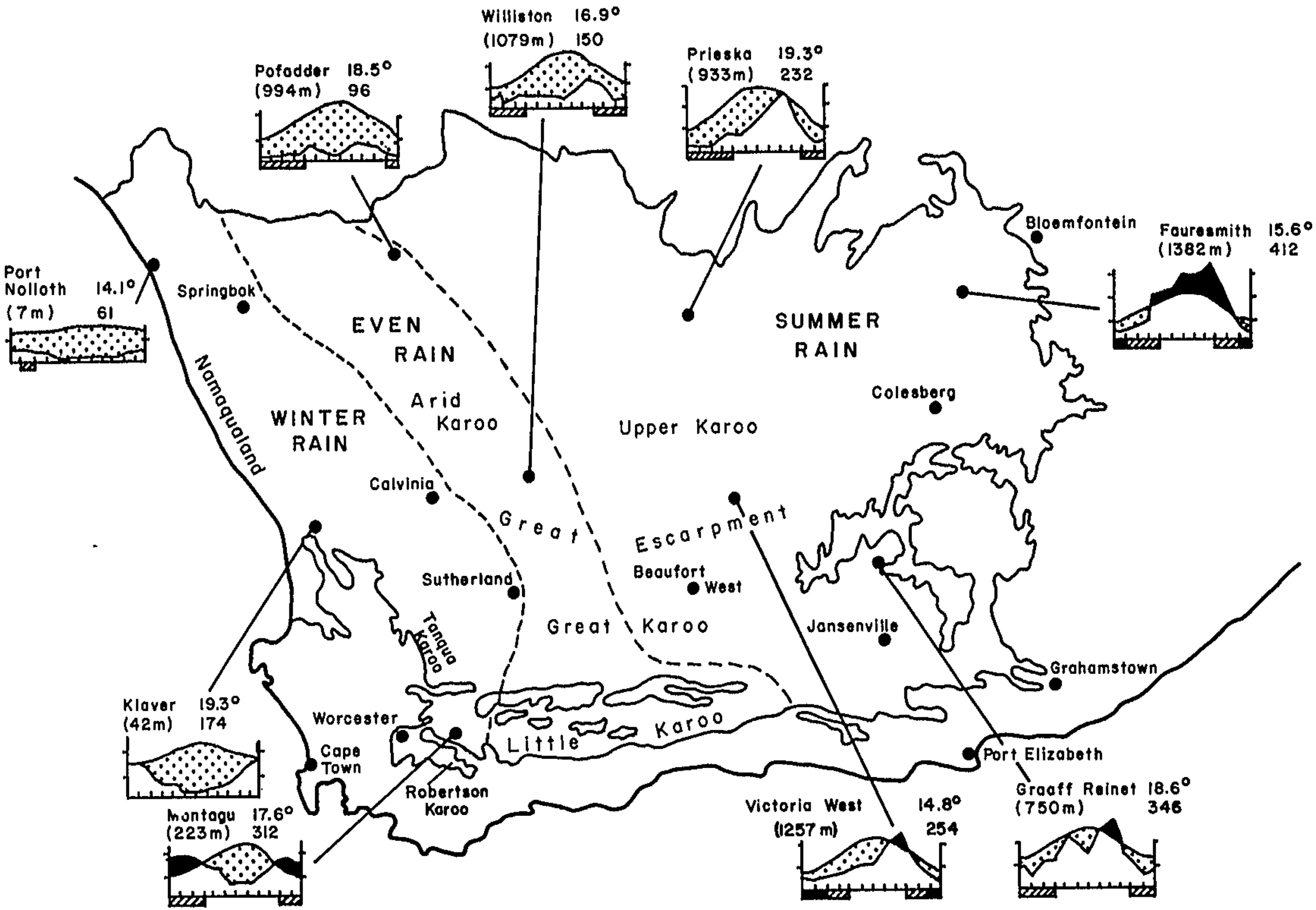

FIGURE 2. Climate, topography and principal localities in the karoo biome.

FLORA AND VEGETATION

White (1983)' estimates the richness of the Karoo-Namib flora at 3 500 species, of which more than 50% are endemic. However, there are more than 4 300 species (including subspecific taxa) in Namaqualand alone (A le Roux, personal communication) and a total of 7 000 species for the biome is probably more realistic. Many taxa, particularly in the Mesembryanthemaceae, are in need of revision, so it will be some time before the full complement of the karoo flora can be assessed reliably.

The Karoo-Namib flora is overwhelmingly dominated by the Asteraceae, Mesembryanthemaceae (western and southern regions), Poaceae (particularly Stipeae), Aizoaceae, Asphodelaceae and Scrophulariaceae (Werger 1978). In addition to the numerous genera in the Mesembryanthemaceae (see Herre 1971), Werger (1978) and White (1983) list many other endemic genera. Dominant karoo genera within common growth forms are listed in Table 1. Hilton-Taylor (1986) provides a detailed account of the composition and origins of the karoo flora.

Extensive accounts of karoo vegetation are given by Acocks (1953) and Werger (1978). Table 2 shows the allocation of Acocks's (1953) veld types within the biome. Structurally karoo vegetation can be characterized as a dwarf open shrubland (sensu Campbell et al 1981). Fire is unimportant in the Karoo except in the grassy eastern regions where occasional fires after a sequence of good rain years may exert a dramatic influence on vegetation structure (Huntley 1984).

A unique feature of the biome is the overwhelming dominance of dwarf and low succulent shrubs in the winter rainfall regions of the south-west and west. Here there has been extensive speciation within the Mesembryanthemaceae (c 1 500 species) and other succulent taxa including _Aloe_, _Anacampseros_, _Cotyledon_, _Crassula_, _Euphorbia_, _Gasteria_, _Haworthia_, _Huernia_, _Sarcocaulon_ and _Stapelia_ (Court 1981; White 1983; Hilton-Taylor 1986). Eastwards in the Great and Upper Karoo, succulents are less conspicuous and dwarf deciduous shrubs belonging to the Asteraceae (_Eriocephalus_, _Pentzia_, _Pteronia_ etc), predominate. Grasses (_Eragrostis_, _Stipagrostis_) may be common and even dominate, depending on soil, rainfall and grazing intensity. In the northern fringes of the biome, near the boundary of the Sudano-Zambezian Region, the dwarf shrubland has an overstorey of subtropical shrubs and trees including deciduous (_Acacia erioloba_, _A mellifera_ ssp _detinens_) and evergreen (_Boscia albitrunca_, _Olea europeae_ ssp _africana_) species. The north-eastern Karoo is transitional to the Highveld grassland and is expanding into that area at an alarming rate (Acocks 1953; Jarman and Bosch 1973). The south-eastern Karoo has strong subtropical thicket affinities and numerous evergreen sclerophyll shrubs and trees of tropical affinity (_Euclea undulata_, _Pappea capensis_, _Rhus undulata_, _Schotia afra_) are an overstorey to a _Pentzia incana_ dominated dwarf shrubland. Although the karoo and fynbos floras have many common genera, vegetation boundaries between karoo and fynbos are distinct and are usually associated with the shale-quartzite interface. However, there is a strong karroid component in the renosterveld communities on the shaley coastal forelands of the fynbos biome (Werger 1978; Cowling 1983).

TABLE 1. Dominant growth forms in the karoo biome

Growth form	Life form	Leaf consistency[1]	Dominant genera	Biogeographical affinity
Annuals	Therophytes	Orthophyll, succulent	Arctotis, Aristida, Cotula, Crassula, Dimorphotheca, Felicia, Heliophila, Hermannia, Grielum, Mesembryanthemum, Nemesia, Osteospermum, Senecio, Ursinea	Karoo-Namib, Cape
Geophytes	Cryptophytes	Orthophyll	Babiana, Bulbine, Ferraria, Homeria, Moraea, Lachenalia, Lapeirousia, Ornithogalum, Oxalis	Karoo-Namib, Cape
Grasses	Hemicryptophytes	Orthophyll	Aristida, Digitaria, Ehrharta, Enneapogon, Eragrostis, Oropetium, Sporobolus, Stipagrostis	Karoo-Namib, Sudano-Zambezian
Dwarf (0-0,25m) and low (0,25-1,0m) deciduous shrubs[2]	Chamaephytes	Orthophyll, fleshy	Didelta, Eriocephalus, Felicia, Galenia, Helichrysum, Hermannia, Indigofera, Lebeckia, Lightfootia, Lycium, Monechma, Nestlera, Osteospermum, Pentzia, Plinthus, Pteronia, Rosenia, Selago, Sutera, Wahlenbergia, Walafrida	Karoo-Namib
Dwarf and low evergreen shrubs	Chamaephytes, Phanerophytes	Fleshy, sclerophyll	Barleria, Berkheya, Chrysocoma, Elytropappus, Eriocephalus, Euryops, Felicia, Gnidia, Helichrysum, Hermannia, Pteronia, Relhania, Selago	Karoo-Namib, Cape
Dwarf and low succulent shrubs	Chamaephytes	Succulent	Aloe, Anacampseros, Andromischus, Conophytum, Cotyledon, Crassula Drosanthemum, Eberlanzia, Euphorbia, Haworthia, Hoodia, Lampranthus, Malephora, Othonna, Psilocaulon, Ruschia, Sarcocaulon, Senecio, Sphalmanthus, Stapelia, Zygophyllum	Karoo-Namib
Mid-high (1-2m) and tall (>2m) deciduous shrubs[3]	Phanerophytes	Orthophyll	Acacia, Combretum, Commiphora, Ehretia, Grewia, Lycium, Rhigozum, Rhus	Sudano-Zambezian, Karoo-Namib
Mid-high and tall evergreen shrubs	Phanerophytes	Sclerophyll	Boscia, Carissa, Diospyros, Euclea, Heeria, Maytenus, Pappea, Rhus, Schotia	Tongaland-Pondoland Sudano-Zambezian
Mid-high and tall succulent shrubs	Phanerophytes	Succulent	Aloe, Cotyledon, Crassula, Euphorbia, Pachypodium, Portulacaria	Karoo-Namib, Tongaland-Pondoland

[1]Consistency classes according to Cowling and Campbell (1983)
[2]Deciduous shrubs include shoot, branch and leaf shedders (Orshan 1953)
[3]Deciduous shrubs include leaf shedders only

TABLE 2. List and characteristics of Acocks's (1953) Veld Types occurring in the karoo biome (sensu Huntley 1984)[1]

Biome	Area[2] km^2	Area[2] %	Veld Types[3]	Annual rainfall (mm yr^{-1}) and seasonality	Structural characterization[4]	Dominant life forms	Dominant growth forms[5]
Succulent Karoo	81908	6,7	26[a],28[a],31[a] 33[a],34[c],39[a] 43[a,c]	20-290 even, winter, strong winter	Dwarf-low open-sparse succulent shrubland	Chamaephytes	Dwarf and low succulent shrubs, annuals, dwarf and low deciduous shrubs, geophytes
Nama-Karoo	346107	28,4	16,17[d],24 26[b],27,28[b] 29,30,31[b] 32[d],33[b],35 36,37[d],38 39[b],40[d],41 42,43[b,c],58[e]	100-520 even, summer, strong summer	Dwarf-low open-sparse grassy shrubland	Chamaephytes, hemicryptophytes	Dwarf and low deciduous shrubs, grasses, dwarf and low succulent shrubs

1 Data compiled largely from Rutherford and Westfall (1986)
2 Area within South Africa
3 Veld type also present in [a]Nama-Karoo Biome, [b]Succulent Karoo Biome, [c]Fynbos Biome, [d]Savanna Biome, [e]Grassland Biome
4 According to Campbell et al (1981)
5 Listed in order of importance; see Table 1

FAUNA

The karoo biome does not comprise a distinct zoogeographic region. The vast migratory herds of large mammals, including springbok (Antidorcas marsupialis), quagga (Equus quagga), black wildebeest (Connochaetes gnou) and blesbok (Damaliscus dorcas phillipsi) have long since disappeared. About 19 species of birds are largely confined to the biome (Huntley 1984). The Karoo also has a rich rodent and reptile fauna; the richness of the tortoise fauna is unsurpassed.

Very little is known about the insect fauna but it is probably very rich and complex in terms of guild structure. The impact of certain species is such that they compete with domestic stock for forage and are thus termed pests. One of these is the karoo caterpillar (Loxostega frustralis) for which Pentzia, a very common dwarf shrub, is the major host plant (Möhr 1982). Swarms of brown locusts (Locustana pardaline) can also cause considerable damage as do harvester termites (Hodotermes mossambicus) (Vorster and Roux 1983).

PLANT-HERBIVORE DYNAMICS: A SPECULATIVE OVERVIEW

Since the karoo biome is mainly a region of extensive stock production, the development of grazing management models of accurate predictive power is a priority. This section outlines briefly some of the theoretical aspects of plant-herbivore dynamics in semi-arid rangelands. Where possible, reference is made to data from the Karoo, in an attempt to provide a speculative overview of plant-herbivore interactions for the biome.

Rainfall: the driving variable

The driving variable in arid and semi-arid ecosystems is rainfall, whose timing, magnitude and spatial patterns are not only discontinuous but also highly stochastic (Noy-Meir 1973). The consequent unpredictable variation in soil moisture exerts a profound effect on biological activity and hence ecosystem functioning. If models are to be realistic, they cannot ignore this stochastic input.

Plants

A low rainfall regime characterized by stochastic inputs is the major selective determinant of morphological, physiological and life history traits of plants of the Karoo and other semi-arid regions (cf Westoby 1980). Rain, falling at different times of the year, and occurring as both small and large events, will affect plant species and growth forms differentially in terms of growth, reproduction and establishment. In the eastern Karoo, substantial spring and summer rains favour the growth and establishment of perennial grasses whereas autumn, winter and late spring rains favour shrubs (Roux 1966). Similarly the establishment and growth of annuals with varying temperature requirements for germination and photosynthesis will be determined by the timing and length of periods of high soil moisture. Annuals usually predominate in areas of strongly seasonal rainfall where there is a high probability of good follow-up rains after the drought is broken (Westoby 1980), eg Namaqualand (Van Rooyen et al 1979).

Both prolonged droughts and a series of unusually high rainfall events will leave their stamp on the composition of the vegetation years or even decades after these rare occurrences (Westoby 1980; Zedler 1981). An unusually severe drought in the Richtersveld resulted in the death of between 80 and 100% of the succulents at one site (Von Willert et al 1985). Perennial grasses do not survive extended droughts in the eastern and Upper Karoo as do many deeper rooted shrub species (Vorster and Roux 1983). The impression is of high population instability, even in the relatively short term, as species respond differentially to particular sequences and combinations of climatic conditions. However, individuals of many plants of semi-arid regions persist as seeds stored on the plants (eg Mesembryanthemaceae) or in the soil. Germination cues are complex and varied, both within and between species (eg Henrici 1935, 1939; Ihlenfeldt 1971; Hobson and Jessop 1975). In certain karoo shrubs, which may flower several times in the year depending on rainfall (eg Pentzia incana) (Bosch 1986), there is great variation in the germination responses of different seed crops (Henrici 1935, 1939). The ability of species to endure droughts as long-lived seeds imparts a resilience on their populations which is broken only by the depletion of seed banks.

In summary, a typical patch of karoo veld comprises a variety of species of different growth forms whose persistence is determined by their physiological and demographic responses to stochastic moisture inputs. This indeterminancy has important implications for systems dynamics and grazing management. These I discuss below.

Herbivores

Defoliation has important effects on the physiological and demographic responses of karoo plants. Frequent defoliation of karoo shrubs reduces significantly shoot and root production as well as reproductive output (Henrici 1951; Hobson and Sykes 1980). Continuous grazing of palatable species may supress or depress flowering, thus preventing further contribution to the seed bank. If the seed bank is depleted local extinction may occur.

Defoliation may also promote seedling establishment, through the suppression of allelopathic effects after the removal of foliage (Hobson and Jessop 1975). In grazed areas hoof action can improve soil permeability on some soil types and create safe sites for germination.

Phytophagous insects may reduce severely the fodder supply of karoo veld (Vorster and Roux 1983). The population bursts observed for many phytophages in the Karoo are probably linked to a specific sequence of climatic events (cf Strong et al 1984).

Karoo veld is characterized by high seasonal and annual variation in forage quality and quantity (Vorster and Roux 1983). In pre-settlement times the migratory behaviour of indigenous ungulates and aboriginal herdsmen would have resulted in a patchy distribution of animals throughout the landscape.

Severe defoliation could be followed by many years of low intensity grazing depending on the demographic responses of herbivores to spatially and temporally variable climatic sequences. Following a severe drought, it seems likely that some time would elapse between the first good rains and the build up of indigenous herbivore numbers to pre-drought levels. The period of relatively low herbivore pressure and optimum plant growth conditions could well have been crucial for seed production and seedling establishment. It is difficult, using fencing and livestock concentrated over relatively small areas, to simulate the defoliation regime under which karoo plants evolved. It is certainly unrealistic to recommend stock densities at levels based upon "equilibrial" estimates of forage supply.

Management implications

The classical concepts of climax and succession are not relevant for semi-arid rangelands (Noy-Meir 1973; Westoby 1980). Predictable series of species replacements are not possible in a system whose dynamics are governed by stochastic climatic inputs and which is prone to irreversible changes resulting from soil erosion (Tidmarsh 1948). Management models must account for the complex dynamics of karoo vegetation and shun unrealistic bias towards determinancy. Models of the latter type will undoubtedly lead to overexploitation.

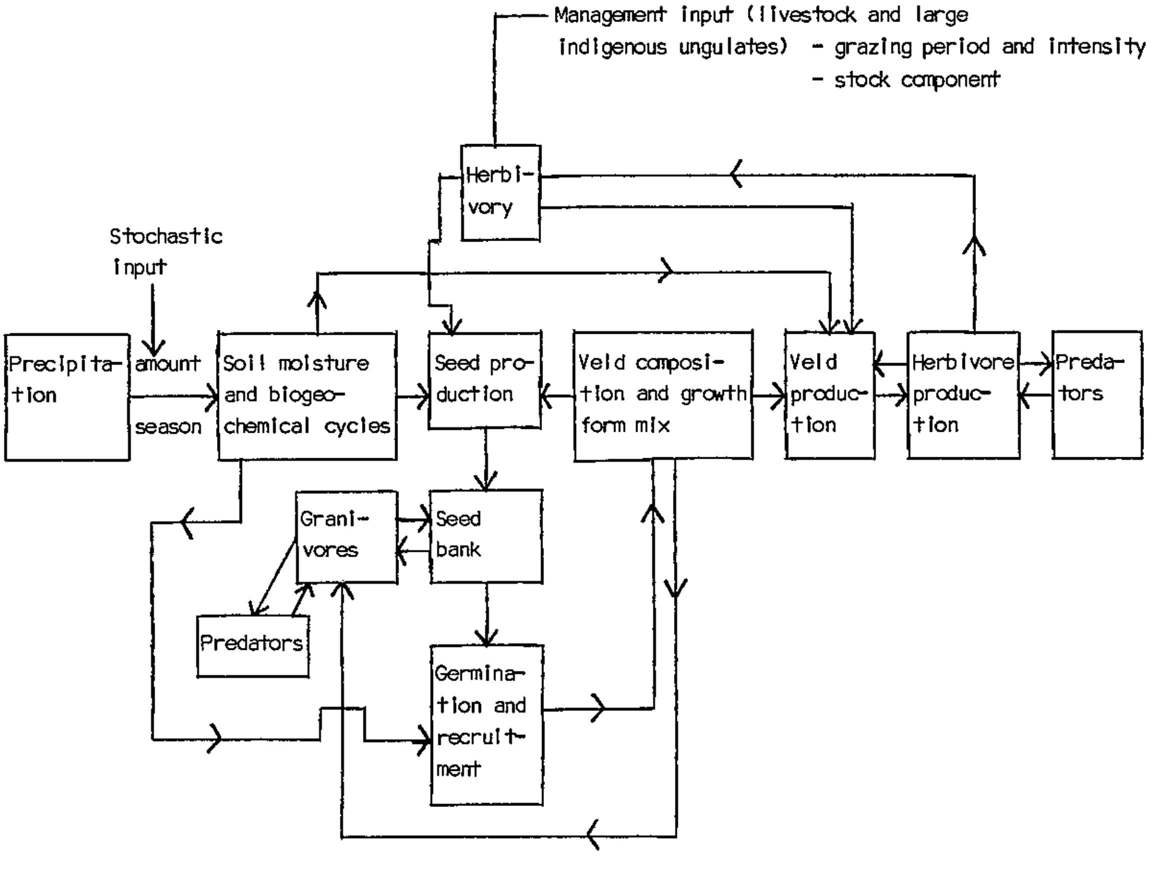

FIGURE 3. Schematic outline of some processes determining composition and production potential of a patch of karoo veld of uniform soil type and veld condition.

Given the short-term economic incentives for the overutilization of karoo veld (Vorster et al 1983), is it possible to find technical solutions to the problems of pastoralism in the Karoo (cf Mentis 1984)? One probably unrealistic solution is to simulate pre-settlement grazing patterns by removing fences and creating migratory cells of livestock at a landscape, rather than a farm-unit level. A more feasible option is to gain a predictive understanding of the physiological and demographic responses of karoo plants in relation to climatic events and defoliation intensity and frequency. Particular attention should be given to grazing during rare climatic events which exert a profound influence on vegetation dynamics (Westoby 1980). Some interactions which should be studied in detail are outlined in Figure 3.

ECOLOGICAL PROBLEMS IN THE KAROO BIOME

VELD DETERIORATION

The overriding ecological problem in the karoo biome is the deterioration of veld resources as a result of inappropriate veld and stock management practices. Dramatic changes have occurred in the composition and extent of karoo veld (Roux and Vorster 1983b). Although aboriginal hunter-gatherers and herdsmen undoubtedly contributed to veld damage (Sampson 1985), deterioration was accelerated, and perhaps made irreversible, after the establishment of a livestock industry in colonial times. Important changes include the spread of karoo veld into marginal grasslands, particularly in the south-western Orange Free State where 66 000 km^2 of former grassland are now encroached (Huntley 1984). Other changes involve the encroachment of undesirable plants (eg Acacia mellifera ssp detinens, Rhigozum trichotomum) and the elimination of desirable ones (Cenchrus ciliaris and other Poaceae, Felicia ovata, Portulacaria afra). Many alien plants (Opuntia spp, Prosopis spp) have become established over vast areas of the Karoo. Their control requires urgent attention.

SOIL EROSION, DESERTIFICATION AND DESERTIZATION

A consequence of reduced plant cover is increased soil erosion which may ultimately lead to irreversible changes in soil structure and desertification. The expansion of desertified areas (desertization) is occurring at an alarming rate in the arid western and central parts of the Karoo (Acocks 1953, 1964; Roux and Vorster 1983b; Tidmarsh 1948).

CONSERVATION

The conservation status of the karoo biome is very poor (Jooste 1986, Table 3) and the area conserved is the lowest of all South African biomes (Rutherford and Westfall 1986). Despite the inadequacy of the veld type (Acocks 1953) as a conservation unit, it is nonetheless instructive to note that only one of the 20 karroid veld types has more than 5% of its area conserved, 10 have less than 1% conserved, and seven have no areas officially conserved (Jooste 1986). Furthermore, the possibility of re-establishing pre-settlement animal communities and grazing patterns exists for only three reserves which are larger than 15 000 ha. Clearly, large biosphere reserves are urgently required to improve the conservation status of the biome.

The western and southern regions of the biome contain a rich and endemic succulent flora of which a high proportion of taxa have very narrow distributions (Hilton-Taylor 1986). Collectors and habitat degradation pose a threat to the continued existence of many taxa. Only very small areas of succulent karroid types are currently conserved (eg Succulent Karoo: 0,17%; Namaqualand Broken Veld: 0,23%; Western Mountain Karoo: 0,24%) (Jooste 1986, Table 3).

TABLE 3. Conserved areas in the karoo biome[1]

Responsible organization	Nama Karoo		Succulent Karoo	
	km^2	% of biome	km^2	% of biome
National Parks Board	403	0,12	0	0
S A Defence Force	1 242	0,36	251	0,31
OFS Provincial Administration	356	0,10	0	0
Cape Provincial Administration	359	0,10	75	0,09
Cape subsidized private reserves	74	0,02	61	0,07
TOTAL	2 434	0,70	387	0,47

[1]Data from Rutherford and Westfall (1986) according to areas derived from the NAKOR National Plan for Nature Conservation: register of conserved areas, October 1984

PROJECT GOALS

The overall goal of biome projects within the CSIR's National Programme for Ecosystem Research is to develop a predictive understanding of the structure and functioning of ecosystems as a basis for their optimal management. This goal statement applies directly to the Karoo Biome Project. Almost the entire Karoo is used for extensive pastoralism and the region supports the country's largest small-stock industry. An understanding of ecological patterns and processes in karoo ecosystems is essential for the management for sustained and high quality yield of veld resources.

Research by range scientists has addressed the major ecological problems associated with veld utilization and deterioration, soil erosion and desertification. However, a strongly applied approach, largely concentrating on the plant-livestock interface, has meant that some important components of karoo ecosystems have been ignored. The Project will be aimed at complementing existing agro-ecological research by providing the structure and support for research on all aspects of karroid ecosystems.

The attainment of the central goal of the Karoo Biome Project will be approached by the:

1. Synthesis of available information on the structure and functioning of karoo ecosystems.

2. Identification of research priorities.

3. Launching of new research projects to enhance the scientific understanding useful in finding solutions to research priorities.

The above activities will be supported by the Foundation for Research Development through the:

1. Organization, funding and coordination of research to improve communication, stimulate cooperation and avoid duplication.

2. Continuous re-evaluation of research progress and priorities through communication at research meetings and specialist working groups.

PROJECT STRUCTURE AND RESEARCH STRATEGY

No researcn programme is without conceptual biases. These may develop, appropriately so, in response to the nature of the ecological problems of the system under study. More often they arise from the biases of "prime movers" within the programme or as a result of adherence to currently fashionable paradigms. An important conceptual debate is between adherents of the population reductionist and those of the ecosystem holist approach to the study of ecosystems (McIntosh 1982). The former approach treats the ecosystem as the sum of its parts (species), whereby insights into the structure and functioning of that system can be derived from studies of populations and their characteristics as products of natural selection. The latter approach emphasizes emergent properties of ecosystems by viewing these systems as developing evolutionary entities largely independent of species components (Smith 1975). This approach, which has a strong energetics and biogeochemical cycling focus, was fostered by the International Biological Programme (IBP). Recently, its contribution to ecology has been severely criticized (eg Simberloff 1982).

On closer scrutiny it becomes clear that differences between the reductionist and ecosystem approaches can be identified as a matter of scale (Allen and Starr 1982). This is particularly true if an hierarchical view of biological phenomena is espoused (Figure 4). Each level of integration in ecology (eg population, community) has its own laws, spatial and temporal scales and patterns which control processes (Allen and Starr 1982; Vrba and Eldredge 1984). The appropriate research level should be dictated by the nature of the ecological problem under investigation. Predictions from models developed at the focal level can be tested by observing pattern and process at upper or lower levels in the hierarchy (upward and downward causation respectively). Every effort should be made to consider the interface between levels. In this way it should be possible to prevent the dogma of any particular approach (eg reductionism, ecosystem holism) from dominating the project.

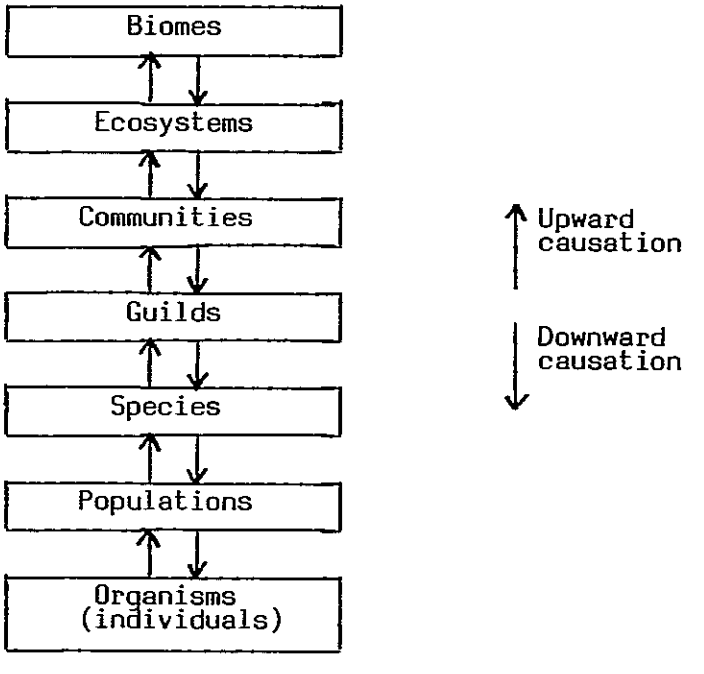

FIGURE 4. Levels of integration in ecology.

Table 4 shows research fields and corresponding levels appropriate for the Karoo Biome Project. No attempt has been made to formally phase the project (cf Anon 1975; Huntley 1978; Kruger 1978; Mentis and Huntley 1982), although it is clear that an understanding of processes at or below the guild level will be necessary for a comprehension of processes at higher levels. A phase approach is not only unrealistic but also places too many restrictions on a research programme which must be opportunistic in terms of available manpower and episodic events (eg locust plagues, extraordinary rainfall events etc).

TABLE 4. Research fields and corresponding levels appropriate for the Karoo Biome Project

Field	Level	Approach
Ecosystem description	Various	Analytical
Historical biogeography and Quaternary vegetation change	Species, community, ecosystem, biome	Analytical
Adaptive physiology and behaviour	Individual, population, species, guild	Analytical
Reproductive ecology, population dynamics and species interactions	Population, species, guild	Analytical
Community processes	Community	Synthetic
Ecosystem models	Ecosystem, biome	Synthetic

Modelling is considered an essential part of the Karoo Biome Project and should reflect the blend of reductionism and holism necessary for the Project's success. Ecologists have too often developed ecosystem models without sufficient regard for the mechanisms of processes or the natural history of organisms. A further problem with models, particularly those focusing on ecosystem dynamics, is that the level of reduction is often too crude. This can be avoided by developing sub-models at the level of populations, species or guilds which can then be incorporated into community or ecosystem models. Therefore modelling at the ecosystem level should ideally await more detailed work on the physiology and biology of species (preferably collapsed into guilds). However, broad conceptual models which function as working hypotheses should not be shunned. Descriptive studies should enjoy priority since they allow model predictions to be extrapolated to areas with similar species and ecosystem properties.

The principal objective of the Project is to provide the fundamental understanding of ecosystem structure and functioning necessary for optimal management of the Karoo. Although the major problems in the karoo biome are agro-ecological they will not be fully comprehended without giving attention to theoretical issues such as resource limitation, equilibrium, optimization, competition and the like. Theoretical and applied researchers should be encouraged to interact so as to allow a productive interplay between theory and experiment and to emphasize the evolutionary significance of adaptations and processes. In this respect, the adaptationist viewpoint (Gould and Lewontin 1979) is valid if carefully and properly pursued (Mayr 1983). Mayr (1983) forcefully stresses the heuristic value of the adaptationist programme, which if applied in the areas of ecophysiology, behaviour, reproductive biology and species interactions, should lead to fascinating insights into the adaptations of karroid organisms to a semi-arid environment.

Attention should be given to research carried out in other deserts and semi-deserts of the world. Parts of the Karoo appear strongly convergent with American, Australian and Eurasian arid lands. The south-eastern Karoo shares a similar climate and vegetation structure with the Argentinian Monte and Arizona Sonoran deserts (cf Orians and Solbrig 1977). Convergence of ecosystem patterns and processes is possible between Namaqualand and other mediterranean deserts such as the Mojave and Negev (cf Shmida and Whittaker 1979). Nonconvergences should provide insights into unique features of the karoo biome. Over the past decade there have been a number of reviews of desert ecology (eg Noy-Meir 1973; Brown 1974; Prakash and Ghosh 1975; Goodall 1976; Goodall et al 1981; Orians and Solbrig 1977; Brown et al 1979; Turner and Kramer 1980; Wallwork 1982; West 1983; Evenari 1985) which should be consulted by Project participants for research approaches and hypotheses.

RESEARCH FIELDS

ECOSYSTEM DESCRIPTION

Rationale

Descriptive studies should be designed to answer the questions "What is the Karoo and how can it be characterized in terms of biotic and abiotic attributes and environments?" The end product of many of these studies will be inventories. However, an analytical approach employing multivariate and correlative methods such as classification, ordination, gradient analysis and multiple regression should be used to summarize data and generate hypotheses. These data will identify research priorities for experimental studies.

Climate and soils: The climatic and pedological environment of the Karoo is highly variable and inadequately described in the literature. A comprehensive classification of land types in terms of climate and soils (see Vorster 1985) is essential for extrapolation from site-bound studies. Detailed descriptions of biogeochemical and hydrological cycles, and meso- and microclimate should be incorporated into site-bound physiological, population and community process studies.

Key questions

(i) What is the range and diversity of climates and soils in the Karoo and how are these correlated with the distribution of major vegetation types?

(ii) What are the major climatic and soil gradients across the biome and how do these affect ecosystem structure?

(iii) What is the long-term variability in amount and seasonality of rainfall within climatic types? Particular attention should be given to the occurrence of small- and large-scale rainfall events and prolonged droughts.

(iv) What are the distribution patterns and abundance of surface and ground water in the biome?

(v) What is the composition, distribution and abundance of microorganisms in different soil types?

Existing research projects[1]

Numbers 27, 50, 62, 82.

Vegetation and flora: The Karoo has a rich flora and a great diversity of vegetation types. Although Acocks's (1953) treatment of karoo veld types is more detailed and less controversial than that of adjacent biomes, a formal characterization of karoo vegetation is lacking. An assessment of the adequacy of Acocks's veld types is required for conservation and

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[1]A list of existing research projects starts on page 25.

land-use planning and also for extrapolation of results from site-bound studies. Data on biogeographic patterns, centres of endemism and nodes of species richness are required for conservation planning and historical biogeographical studies. Syntaxonomic studies should be located in core regions which readily facilitate extrapolation. Systematic studies on economically and ecologically important taxa (eg Pentzia, Lycium and Mesembryanthemaceae) should be encouraged.

Key questions

(i) What are the definitive floristic and structural-functional attributes of karoo vegetation in relation to vegetation from adjacent biomes?

(ii) Is the present system of veld types an adequate treatment of karoo vegetation; what refinements to this scheme are necessary?

(iii) What is the extent of the biome and can major boundaries be mapped using aerial photography and satellite imagery?

(iv) What are the major floristic and structural communities in key areas of the biome?

(v) What are the phytochorological divisions, centres of endemism and nodes of species richness within the biome?

(vi) What are the systematics of important plant groups?

(vii) How do floristic (composition, diversity, phytochorological affinities) and structural-functional (biomass, growth forms, modes of dispersal) attributes of karroid vegetation vary along environmental and disturbance gradients?

Existing research projects

Numbers 3, 9, 10, 11, 14, 19, 20, 21, 23, 27, 29, 30, 48, 49, 50, 57, 58, 60, 67, 71, 72, 77, 79, 82, 90, 92, 91.

Fauna: Although the distribution patterns, habitats and community structure of certain groups are quite well known, data are lacking for others, many of which are ecologically important (eg invertebrates and rodents).

Key questions

(i) What are the zoogeographical affinities and composition of the karoo fauna?

(ii) What are the centres of endemism, nodes of richness and distribution tracks (patterns) of animal groups within the biome?

(iii) What are the systematics of ecologically important animal groups (particularly invertebrates)?

(iv) What are the effects of plant community structure on the abundance and diversity of animal species?

(v) How does the composition, diversity and structure of faunal communities vary along environmental and disturbance gradients?

Existing research projects

Numbers 1, 4, 6, 7, 17, 31, 35, 54.

Land use: The principal form of land use in the Karoo is livestock production; stocking rates and livestock types vary across the biome. Planners require information on the conservation worthiness of different areas, land-use patterns and the proportion of conserved, well-managed and degraded veld. A knowledge of the effects of different forms of land use on plant and animal community structure will lead to the formulation of hypotheses and appropriate experimental tests.

Key questions

(i) What are the proportions of land subject to different forms of land use and how much land is degraded?

(ii) Do the conserved areas of the biome afford adequate protection for rare and threatened plants, animals and habitats?

(iii) What socio-economic conditions inhibit the application of rational land-use practices?

(iv) What are the economic and production potentials of different forms of land use (eg small stock production, game ranching) in karoo veld types?

(v) Are there reliable plant and animal indicators for different forms of land use and environmental degradation?

Existing research projects

Numbers 19, 22, 45, 46, 47, 82.

HISTORICAL BIOGEOGRAPHY AND QUATERNARY VEGETATION CHANGE

Rationale

Floras and faunas of arid and semi-arid regions have been evolving in association with climatic deterioration since the early Tertiary, but the most spectacular bursts of speciation and shifts in vegetation boundaries have probably occurred in the climatically unstable Pleistocene (Beard 1976; Solbrig 1976). The reconstruction of Pleistocene and Holocene environments and vegetation patterns provides the historical background for contemporary vegetation change and therefore has management implications. In addition to other lines of evidence, emphasis should be given to the role of phylogenetic systematics in the formulation of historical biogeographic hypotheses.

Key questions

(i) What are the major distribution tracks of the karoo biota and what are their directions as evidenced from phylogenetic studies of key taxa?

(ii) Can present biogeographical zones, centres of endemism and nodes of species richness be explained by historical events?

(iii) What were the extent and nature of changes of karoo vegetation and associated fauna during the Pleistocene and Holocene as predicted by biogeographic analyses of contemporary flora and fauna, archaeological, geomorphological, palaeontological and palynological data?

(iv) What were the impacts of Khoi-San and early European culture on the karoo environment?

Existing research projects

Numbers 16, 58, 62, 65, 66, 67, 75, 82, 90, 92, 93, 94, 95.

ADAPTIVE PHYSIOLOGY AND BEHAVIOUR

Rationale

Arid and semi-desert environments produce some of the most interesting adaptations in plants and animals. Research is required to explain the ecological and evolutionary significance of structural, morphological and behavioural adaptations of karoo organisms. Studies should be rooted in an adaptationist programme which is aware of the pitfalls of extreme reductionism and evolutionary constraints. The most fruitful approach would be to collapse species into functional guilds characterized in terms of physiological, morphological and behavioural attributes. This will make modelling at the community level both easier and more accurate.

Key questions

(i) What is the adaptive significance of structural attributes of karoo plants in relation to temperature, insolation, moisture and defoliation stresses?

(ii) What is the adaptive significance of the morphology, physiology, colouration and behaviour of karoo animals in relation to heat and moisture stress and other limiting factors?

(iii) What are the easily recognizable and biologically realistic functional guilds of karoo plants and animals?

(iv) What are the modes of CO_2 assimilation, respiration, photo-respiration, carbon allocation and production of plant species of different functional guilds in relation to diurnal and seasonal cycles of above-ground environmental conditions, soil moisture and soil water potential?

(v) What are the water relations (plant water potential, water use efficiency etc) of different plant functional guilds in relation to changes in environmental conditions as for (iv) above?

(vi) What are the patterns of nutrient allocation and cycling of different plant functional guilds in relation to changes in environmental conditions as for (iv) above?

(vii) What are the effects of defoliation on processes (iv) to (vi)?

Existing research projects

Numbers 24, 25, 32, 36, 44, 56, 59, 61, 70, 73, 76, 83, 88, 89.

REPRODUCTIVE ECOLOGY, POPULATION DYNAMICS AND SPECIES INTERACTIONS

Rationale

An understanding of reproductive and population processes of karoo organisms is essential for modelling the dynamics and resilience of karoo communities and ecosystems. The paucity of these kinds of information for the Karoo constitutes an important gap in our knowledge of the biome. Data are required on the reproductive biology of key organisms with special emphasis on the adaptive significance of life history traits which are relevant to an understanding of the dynamics of populations in response to variations in environment and disturbance regime. Attempts should be made to collapse species into life-history guilds.

In the Karoo, research on species interactions has been largely confined to the plant-livestock interface. Research on interspecific interactions should be expanded to incorporate the effects of competition, predation and mutualisms at the population level for all groups of organisms. The biome holds special promise for research on plant-insect-insectivore interactions.

Key questions

(i) Which biotic and abiotic factors affect seed set and clutch size and how are these influenced by changes in the environment and disturbance (particularly grazing) regime?

(ii) What is the relative importance of vegetative *versus* sexual propagation of karoo plants under various climatic and disturbance regimes?

(iii) What conditions of soil moisture and temperature promote germination, seedling establishment and mortality and is there evidence for discrete periods of recruitment and mortality?

(iv) What are the effects of disturbance (particularly grazing) on germination success, seedling establishment and mortality? What are the minimum requirements for the maintenance of viable populations?

(v) What is the location and size of seed banks of various species and guilds? What is the potential availability to, and levels of predation by, different granivores (ants, birds, rodents)?

(vi) Can fluctuations in the populations of phytophagous insects (particularly pest species such as locusts, karoo caterpillar etc) be predicted?

(vii) What is the role of competition and predation on the structure of plant and animal populations? How often are plant resources limited to such an extent that herbivores compete for them?

(viii) What is the role of mutualisms (particularly dispersal) on the maintenance of community structure?

(ix) Which species and what fraction of the plant primary production are eaten by various herbivores and how does this vary seasonally and annually?

(x) What is the effect of plant density, diversity and production on herbivore loads?

(xi) How do herbivores locate host-plants and what are the effects of herbivory on feeding-induced changes in plant defences?

(xii) What is the distribution of defensive secondary compounds in the karoo flora?

(xiii) Are allelopathic effects important in inhibiting germination, establishment and hence spacing of karoo plants?

Existing research projects

Numbers 2, 8, 13, 15, 18, 25, 26, 28, 32, 33, 34, 36, 37, 40, 41, 42, 43, 45, 46, 47, 52, 53, 54, 55, 60, 61, 63, 64, 68, 69, 76, 80, 83, 84, 85, 86, 87.

COMMUNITY PROCESSES

Rationale

A focus on the emergent properties and processes of communities is essential for a synthetic view of their structure and functioning. This part of the project should aim at an accurate computerized simulation of community biomass, growth, production and biogeochemical cycling. Model building will depend on the availability of appropriate sub-models of physiological processes within various functional guilds.

Key questions

(i) What are the patterns of environmental limits to community biomass and productivity?

(ii) What are the patterns of community water, carbon and nutrient cycling and how do these change with disturbance regime? Specifically, how are these processes affected by herbivory, coprophagy and decomposition?

(iii) What are the effects of soil and vegetation structure on hydrological cycling?

(iv) What are the effects of soil micro-organisms on soil properties and nutrient cycling?

(v) Can community structure and diversity be predicted by physiological models of plant growth and competition for resources such as nutrients and water?

(vi) What is the relationship between community processes, particularly productivity, and herbivore loads?

Relevant existing research projects

Numbers 38, 39, 74, 78, 81.

SYNTHESIS: ECOSYSTEM MODELS

Rationale

As the most important part of the Karoo Biome Project, this activity should integrate the results of previous research into synthetic models, evaluate the current state of knowledge, and propose future research directions. Although modelling should be implicit in all research fields of the Project, at some stage the modelling procedure must make an explicit attempt to incorporate the interactive effects of biological, physiological and physico-chemical processes on ecosystem dynamics. A major problem with modelling ecosystems is that the range of natural variability within ecosystems, makes it impossible to completely disprove reasonable generalities.

Irrespective of the research level or area, stochastic variability is likely to be the overriding theme in the karoo biome: modelling attempts should be aware of this.

It must be stressed that the construction of ecosystem models should not be considered the raison d'etre for the Project. Rather, modelling should be viewed as the most parsimonious way of generating a range of possible solutions to the key questions: how do karoo ecosystems work and what are the effects of various disturbances on ecosystem structure and functioning? Real solutions will come from experiments designed to test model predictions and will depend on well coordinated and interdisciplinary research.

EXISTING RESEARCH PROJECTS

Cape Provincial Administration

1. Baard E H W and de Villiers A L. The distribution of reptiles and amphibians of the Cape Province. Cape Department of Nature and Environmental Conservation.

2. Boshoff A F. The long-term stability of a breeding population of the martial eagle Polemaetus bellicosus in a sheep farming area in the Great Karoo. Cape Department of Nature and Environmental Conservation.

3. Boucher C and le Roux A. A vegetation survey of the strand vegetation of the west coast. Botanical Research Institute and Cape Department of Nature and Environmental Conservation.

4. Branch W R. Reptiles and amphibians of the Karoo National Park. Port Elizabeth Museum.

5. Coetzee K. The distribution and habitat preferences of the larger mammals on Rolfontein Nature Reserve. Cape Department of Nature and Environmental Conservation.

6. Coetzee D J and Pool R C. An ecological study of the Cape river shrimp Palaemon capensis (de Man). Cape Department of Nature and Environmental Conservation.

7. Erasmus B H. The distribution of mammals in the northern Cape. Cape Department of Nature and Environmental Conservation.

8. Gess F W, Gess S K and Weaving A J S. Systematic and ecological-behavioural investigations of aculeate wasps and bees (Hymenoptera) in various areas characterized by different but mainly karroid vegetation types. Albany Museum.

9. Gubb A A. Monitoring vegetation change in the northern Cape. McGregor Museum.

10. Gubb A A. Structural and floristic classification of the main vegetation types of the northern Cape. McGregor Museum.

11. Gubb A A. Vegetation of the de Beer farms. McGregor Museum.

12. Gubb A A. Large trees and shrubs of the northern Cape. McGregor Museum.

13. Gubb A A. Vegetation availability and utilization by springbok. McGregor Museum.

14. Gubb A A. Determining the usefulness of remote sensing techniques for mapping vegetation units in the northern Cape. McGregor Museum.

15. Gubb A A. The interrelationship between Acacia erioloba thorns and insects in a northern Cape woodland. McGregor Museum.

16. Hall S L. The Late Stone Age of the Winterberg Escarpment and Fish River Basin. Albany Museum.

17. Hëyl C W, Currie M H and others. Monthly censuses of waterfowl on selected wetlands in the Cape Province. Cape Department of Nature and Environmental Conservation.

18. Jooste J F and Fairall N. A study of the food preference of the springbok Antidorcas marsupialis in its main distribution area. Cape Department of Nature and Environmental Conservation.

19. Laidler D F. A vegetation survey of the karroid veld types of the Little Karoo, with reference to conservation priority areas. Cape Department of Nature and Environmental Conservation.

20. Le Roux A and Lloyd J W. A reconnaissance survey of the vegetation of Namaqualand. Cape Department of Nature and Environmental Conservation.

21. Le Roux A, Willems L and Ramsey M J. A phytosociological study of the Rocherpan Nature Reserve. Cape Department of Nature and Environmental Conservation.

22. Le Roux A and Lloyd J W. 'n Stelsel, en biotiese en abiotiese inligtingsdatabasis, vir die identifisering van potensiële bewaringsgebiede. Kaap Departement Natuur- en Omgewingsbewaring.

23. Le Roux A, Lloyd J W and Gubb A A. A vegetation survey of the Grootvloer - Verneukpan area of the northern Cape. Cape Department of Nature and Environmental Conservation.

24. Le Roux A and Orshan G. Phenomorphological studies of some plants of the Hester Malan Nature Reserve. Cape Department of Nature and Environmental Conservation and the Hebrew University of Jerusalem.

25. Liversidge R. Springbok. McGregor Museum.

26. Liversidge R. Raptors of the Kalahari. McGregor Museum.

27. Lloyd J W. A plant ecological study of the farm "Vaalputs", Bushmanland, with special reference to edaphic factors. Cape Department of Nature and Environmental Conservation.

28. Norton P M. Population dynamics of mountain reedbuck on the Orange River reserves. Cape Department of Nature and Environmental Conservation.

29. Palmer A R. Mapping of karoo vegetation by means of remote sensing. Cape Department of Nature and Environmental Conservation.

30. Palmer A R. Floristic surveys of the Karoo and Commandodrift Nature Reserves. Cape Department of Nature and Environmental Conservation.

31. Richardson P. Vertebrate fauna of the northern Cape. McGregor Museum.

32. Richardson P. The social behaviour of the aardwolf Proteles cristatus - how it relates to its food source and compares with other Hyaenidae. McGregor Museum.

33. Richardson P. Diet of black-backed jackals on Rooipoort. McGregor Museum.

34. Richardson P. Breeding and feeding behaviour of vultures at Dronfield. McGregor Museum.

35. Vernon C J. Distribution status of birds in the eastern Cape. East London Museum.

36. Weaving A J S. Nesting behaviour and prey selection in South African digger wasps of the genus Ammophila. Albany Museum.

Orange Free State Provincial Administration

37. Voster H. Carrying capacity of the False Upper Karoo on the Tussen-die-Riviere Game Farm. Nature Conservation Division.

Department of Agriculture and Water Supply

38. Botha P. Phytomass assessment and production of eleven veld types in the karoo region. Karoo Region.

39. Botha P. Phytomass assessment of vegetation in different phenophases in the Meentspruit farming area. Karoo Region.

40. Botha P. Selective grazing habits of sheep, goats and cattle in the False Upper Karoo. Karoo Region.

41. Botha P. Grazing habits of Angora goats and Merino sheep in the False Upper Karoo. Karoo Region.

42. Botha P. Grazing habits of Afrinos, Merinos and Dorpers near Carnarvon in the arid karoo. Karoo Region.

43. Harding G B. Biology of Prosopis in the karoo. Weeds Laboratory.

44. Moore A and Robertson B L. The ecology and ecophysiology of Rhigozum trichotomum (driedoring). Orange Free State Region.

45. Roux P W. Investigations of principles of management of apron veld in the eastern mixed karoo. Karoo Region.

46. Roux P W. Investigations of principles of management of eastern mixed karoo. Karoo Region.

47. Roux P W. Investigation of principles of management of sandstone and dolerite broken veld in the eastern mixed karoo. Karoo Region.

48. Roux P W. Development of a photographic technique for the evaluation of change in the karoo veld. Karoo Region.

49. Scheepers J C. A revision of karroid and adjoining veld types. Botanical Research Institute.

50. Vorster M. Influence of climate on vegetation in the karoo : six veld types on Grootfontein College of Agriculture. Karoo Region.

51. Vorster M. Chemical control of Prosopis sp in the north-western Karoo. Karoo Region.

52. Zeeman P L. Voluntary intake, digestibility and chemical composition of karoo veld as selected by small stock. Karoo Region.

National Parks Board

53. Moolman L. Strategies of resource utilization by Felis caracal in the Karoo: comparison between diet in the Park and farmland. Mountain Zebra National Park.

54. Novellie P. Herbivore distribution, population structure and habitat selection in the Mountain Zebra National Park.

55. Novellie P. Vegetation changes under the influence of wild herbivores in the Mountain Zebra and Karoo National Parks.

56. Pieterse P C and Novellie P. The relationships between surface stones, soil moisture and plant species composition in the Mountain Zebra National Park.

National Botanic Gardens

57. Bayer M B. Systematics of southern African succulents. Karoo Botanic Garden.

58. Bayer M B and Hilton Taylor C. Biogeography of the karoo flora. Karoo Botanic Garden.

59. Perry P and Orshan G. Phenomorphological studies of some plants in the Worcester Wild Flower Reserve. National Botanic Gardens (Kirstenbosch) and the Hebrew University of Jerusalem.

Rhodes University

60. Court G D. Population dynamics, biogeography and taxonomy of the dactyliferous Euphorbia species with special emphasis on E polycephala. Department of Plant Sciences.

61. Craig A J F K, Hulley P E and Walter G. The comparative biology of redwinged and palewinged starlings in an area of sympatry near Cradock. Department of Zoology and Entomology.

62. Dewey F J. Vleis and vlei sedimentology in the Winterberg, eastern Cape. Department of Geography.

63. Horak I G. Ticks associated with large and small mammals in the Mountain Zebra National Park. Tick Research Institute.

64. Lubke R A. The interactions between mistletoes and their hosts. Department of Plant Sciences.

65. Meadows K F. Holocene vegetation history of Dunedin Vlei, Winterberg, eastern Cape. Department of Geography.

66. Meadows M E. Pollen analysis of vlei sediments in and around the Karoo. Department of Geography.

67. Meadows M E and Meadows K F. Contemporary pollen rain and vegetation of the Winterberg, eastern Cape. Department of Geography.

68. Moran V C. The biological control of jointed cactus Opuntia aurantiaca. Department of Zoology and Entomology.

University of Cape Town

69. Cowling R M. Ecological studies in the south-western karoo: seed bank dynamics, dispersal, germination and recruitment in the Mesembryanthemaceae. Department of Botany.

70. Moll E J and Boschoff C. Phenology of different growth forms in the Worcester Karoo. Department of Botany.

71. Moll E J and Hilton-Taylor C. A phytosociological study of the Worcester Botanic Gardens. Department of Botany.

72. Moll E J, Hilton-Taylor C and Knight R. The phytogeography of Western Cape shrublands. Department of Botany.

University of the Orange Free State

73. Hewitt P H. The carbon, nitrogen and energy economy of the harvester termite Hodotermes mossambicus Hagan. Department of Zoology.

74. Le Roux J S. The rate of decay and erosion in the Wuras Dam area. Department of Geography.

75. Scott L. Pollen analysis of deposits in the Orange Free State. Institute of Environmental Sciences.

76. Van der Linde T C de K. Changes in the wing muscles and reproductive systems of reproducers during the establishment of colonies by Hodotermes mossambicus Hagan. Department of Zoology.

77. Van Rensburg W L J. Phytochemistry of Monsonia, Sarcocaulon and Erodium (Geraniaceae). Department of Pasture Science.

78. Van Rensburg W L J and Snyman H A. Defoliation and moisture studies on perennial grazing plants in the field and glasshouse. Department of Pasture Science.

79. Venter H J T. Taxonomy, morphology, cytology and phytochemistry of Monsonia, Sarcocaulon and Erodium (Geraniaceae). Department of Botany.

80. Vorster L F. Grazing behaviour and rotational grazing of blesbok Damaliscus dorcas phillipsi in the Verwoerd Dam Nature Reserve. Department of Pasture Science.

81. Wiltshire G H. Productivity of reedbeds around a silt-laden dam. Institute for Environmental Sciences.

University of Port Elizabeth

82. Cowling R M and Hoffman M T. Floristics, structure and dynamics of subtropical and karroid shrublands along a climatic gradient in the Sundays River Valley, S E Cape. Department of Botany.

83. Robertson B L and Smith A C. Phenology, reproduction potential and ecomorphology of Rhigozum trichotomum in the Carnarvon and Upington districts. Department of Botany.

University of Pretoria

84. Fairall N and Braak H H. The influence of predators on the dassie population on farming land and a large conservation area. Mammal Research Institute, Department of Zoology, in collaboration with the Karoo National Park.

85. Fairall N, Hanekom N and Braak H H. A comparative study of the population dynamics of hyrax Procavia capensis in the Tsitsikamma and Karoo National Parks. Mammal Research Institute Department of Zoology, in collaboration with the Tsitisikamma and Karoo National Parks.

86. Moolman L C and Bothma J du P. Caracal as a problem animal in the Mountain Zebra National Park and surrounding farm land. Eugene Marais Chair of Wildlife Management, Department of Zoology.

87. Skinner J D and Davies R A G. A comparison of springbok and merino sheep on karoo veld. Mammal Research Institute, Department of Zoology.

88. Van Rooyen M W. Ecophysiological studies of some Namaqualand plant species. Department of Botany.

University of Stellenbosch

89. Joubert J G V. The determination of production of edible karoo plants and the veld on the farm Komkommerleegte in the Fraserburg district. Department of Agronomy and Pastures.

90. Van der Walt J J A, Moll E J, Hilton-Taylor C and Bayer M B. Plant species distributions in the Winter Rainfall Karoo. Botany Department.

University of the Witwatersrand

91. Knox D. The taxonomy and distribution of the genus Xanthoparmelia in southern Africa. Botany Department.

92. Lowry T K. Biosystematic studies of Pteronia. Department of Botany.

93. Lowry T K. General chromosome survey of the Compositae. Department of Botany.

94. Robinson E R and Gibbs Russel G E. Grass speciation in the Karoo. Department of Botany (in collaboration with the Botanical Research Institute).

Southern Methodist University, Dallas

95. Sampson C G. Seacow Valley Archaeological Project, Department of Archaeology.

FUTURE RESEARCH DIRECTIONS AND COORDINATION

In this section I analyse the 95 existing research projects currently underway in the karoo biome in terms of research fields and key questions. Important questions are: to what extent is the current research effort answering key questions outlined above; and how should the Project be coordinated on a regional basis? Constraints on the growth and development of the Project are discussed elsewhere (Cowling 1986).

It is clear that the descriptive component dominates the current research effort (Figure 5). This is not an unhealthy situation for a fledgling biome research programme. However, the bias towards descriptive studies probably reflects the training and research attitudes of the ecological community (cf Huntley 1977) and the research policy of government organizations. Every effort must be made to extract as much information as possible from survey data, particularly in the extrapolation and testing of vegetation concepts. The paucity of descriptive studies on climate and soils is cause for alarm. Detailed meso- and microclimatic studies as well as data on the distribution and properties of soils are essential for

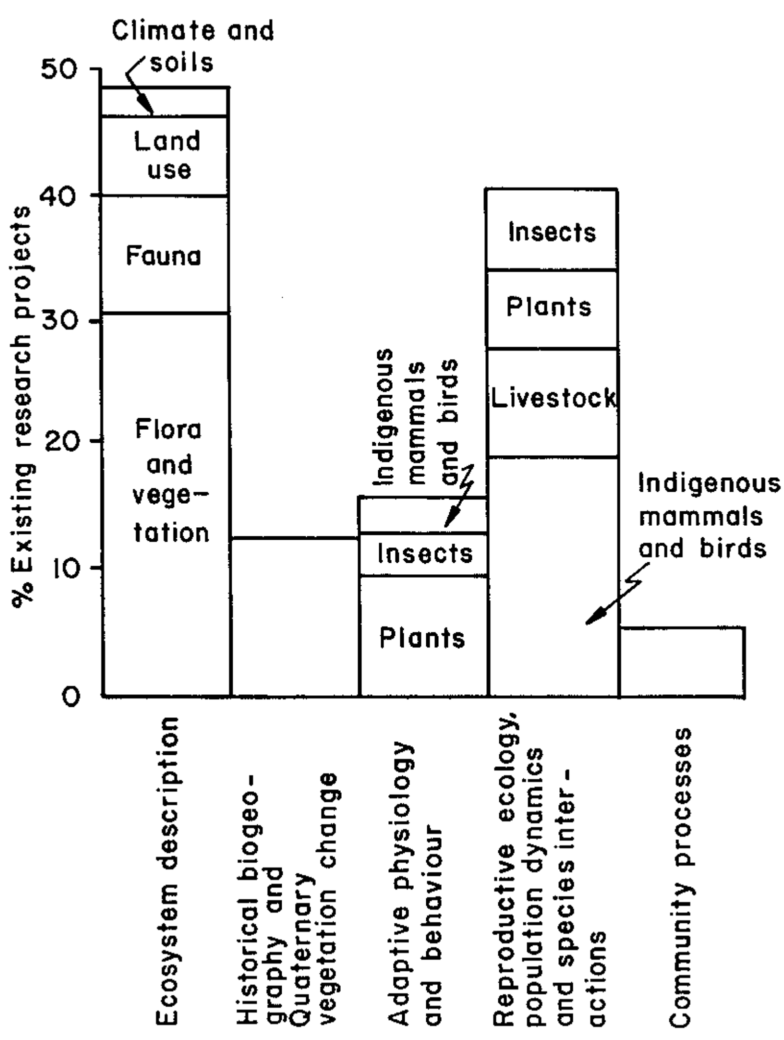


FIGURE 5. Allocation of existing projects in the Karoo Biome Project to research fields.

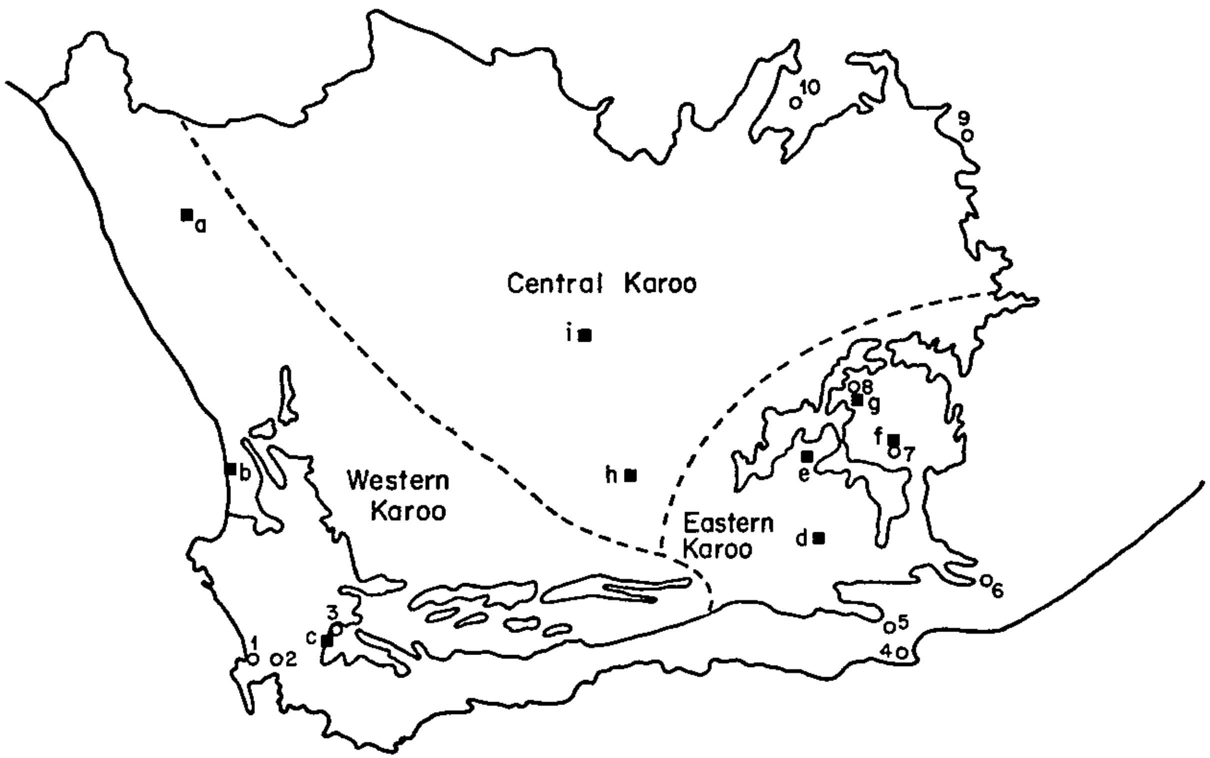
modelling. A synthesis of climatic data, stressing the rainfall variability component, is required. The systematics of ecologically important plant and animal groups, particularly the Mesembryanthemaceae and insects, require urgent attention.

Although historical biogeographic studies comprise a small percentage of the total projects (Figure 5), the biome is fortunate in having a core of able and productive researchers in this field. C G Sampson's Seacow Valley Archaeological Project provides a fascinating insight into the impact of San settlements in the Upper Karoo (eg Sampson 1985). Other research involves palynological studies in the eastern margin of the Karoo (M E Meadows), vegetation history in the south-western (C Hilton Taylor) and south-eastern (M T Hoffman) Karoo, and breeding systems, population genetics and speciation of karoo plants (T K Lowry). There are, however, no systematic studies focusing on the phylogenetic component. Rigorous cladistic analyses are important for the formulation of historical biogeographic hypotheses (Cowling 1985) and will provide insights into the origin and spread of the karoo flora (eg Bremer 1978).

There are very few ecophysiological and behavioural studies of karoo organisms (Figure 5). Growth and production models of different plant guilds under a range of climatic and defoliation regimes are essential for grazing management models. The fascinating adaptive array of karoo plants and animals has hardly been touched upon. With the exception of the excellent research undertaken by D J von Willert and his colleagues at Bayreuth (eg Von Willert et al 1985), virtually nothing is known of the ecophysiology of the Karoo's rich succulent flora. Research on animal groups, particularly insects, small mammals and the herpetofauna, is sadly lacking. The stimulation of good ecophysiological research which is mindful of processes above the organism level, is one of the greatest challenges for the Karoo Biome Project.

The considerable research activity in the field of reproductive ecology, population dynamics and species interactions (Figure 5) does not imply a healthy research effort. There is a disproportionate number of studies on the natural history of larger indigenous mammals and birds, which in most cases do not give sufficient quantitative attention to the plant-animal interface and other interactions. Given the important role of rodents and ants as granivores in semi-arid communities (Brown et al 1979) and the necessity for modelling seed banks in order to predict compositional change (Westoby 1980), the total lack of these kinds of studies in the biome is cause for concern. Other topics in need of study are the germination ecology and population dynamics of selected species and growth forms (eg the annual flora of Namaqualand), plant-insect interactions and the impacts of different defoliation regimes on both plant and animal populations. Much of this research will require long-term field experiments designed to test specific hypotheses (Crawley 1983).

At present few projects address community processes. Intergrated community level studies should ideally await detailed population, growth and productivity sub-models for guilds and species. However, at this early stage it will be necessary to encourage site-bound interdisciplinary studies in order to generate the data required for accurate community and ecosystem simulation models.



Research sites

a. Hester Malan Nature Reserve
b. Nortier Experimental Farm
c. Worcester Veld Reserve
   Worcester Botanic Gardens
d. Jansenville Experimental Farm
e. Karoo Nature Reserve
f. Mountain Zebra National Park
g. Grootfontein Experimental Farm
h. Karoo National Park
i. Carnarvon Experimental Farm

Research personnel and facilities

1. Cape Town
   - University of Cape Town
   - University of the Western Cape
   - National Botanic Gardens
2. Stellenbosch
   - University of Stellenbosch
   - Cape Provincial Administration
   - Dept of Agriculture and Water Supply
3. Worcester
   - National Botanic Gardens
4. Port Elizabeth
   - University of Port Elizabeth
5. Uitenhage
   - Dept of Agriculture and Water Supply
6. Grahamstown
   - Rhodes University
   - Cape Provincial Administration
   - Dept of Agriculture and Water Supply
7. Cradock
   - National Parks Board
8. Middelburg
   - Dept of Agriculture and Water Supply
9. Bloemfontein
   - University of the Orange Free State
   - OFS Provincial Administration
   - Dept of Agriculture and Water Supply
10. Kimberley
   - Cape Provincial Administration

FIGURE 6. Research regions and facilities in the karoo biome.

All research centres and universities are widely scattered on the periphery of the karoo biome (Figure 6). Not only does this increase the costs of research in the heart of the biome but it also makes research coordination and communication costly and difficult. It would be sensible, therefore, to develop cells of research activity in different geographical regions within the biome. The three such regions are the eastern Karoo, the western Karoo and the central Karoo (Figure 6).

The eastern Karoo is an area of great environmental and biological diversity and numerous ecological problems. It should be possible to establish a body of researchers centred at the University of Port Elizabeth, Rhodes University, Grootfontein Agricultural Research Institute and institutes of the Cape Provincial Administration in Grahamstown.

The central Karoo encompasses a vast area characterized by relative climatic and biological uniformity. There are no universities or research institutions in the region. Researchers from the University of the Orange Free State, Orange Free State Provincial Administration (Bloemfontein), Cape Provincial Administration (Kimberley) and the Department of Agriculture and Water Supply (Glen and Grootfontein) should coordinate research activities in the central Karoo.

In addition to the usual problem of veld deterioration, the western Karoo is bedevilled with conservation issues associated with a rich and endemic succulent flora. The Cape Peninsula and environs support three universities which have, up to now, undertaken very little research in the Karoo. The area is also the headquarters for the Cape Provincial Administration's Department of Nature and Environmental Conservation whose reseachers are currently active in Namaqualand and the Little Karoo. There is every reason to expect the development of a strong research community in the western Karoo.

Researchers from the three regions will be convened at annual research meetings to discuss research progress and priorities. However, it will be the responsibility of the communities in each of the regions to encourage communication and organize specialist working groups.

Finally the farming community must be involved as far as possible in the Project activities. Through their long association with the veld, from which they make a living, farmers have gained insights which will be of great value to researchers. In attempting to understand the structure and functioning of karoo communities, the researcher will be providing solutions to the farmer's problems. It is essential that research results are communicated effectively and efficiently to the farming community.

ADMINISTRATION OF THE PROJECT

The Karoo Biome Project is administered within the Terrestrial Ecosystems Section of the CSIR's National Programme for Ecosystem Research by the Steering Committee for the Karoo Biome Project.

Membership of the Steering Committee comprises:

Dr P W Roux (Chairman), Department of Agriculture and Water Supply (Karoo Region)
Dr R M Cowling, University of Cape Town
Mr D Grey, Forestry Branch, Department of Environment Affairs
Mr B J Huntley, CSIR
Mrs M L Jarman, CSIR
Mr D F Laidler, Cape Department of Nature and Environmental Conservation
Prof R A Lubke, Rhodes University
Prof E J Moll, University of Cape Town
Dr H A Snyman, University of the Orange Free State
Prof G K Theron, University of Pretoria
Mr C J Vernon, East London Museum

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