VEGETATION ECOLOGY OF THE CAMDEBO AND SNEEUBERG REGIONS OF THE KAROO BIOME, SOUTH AFRICA.

THESIS

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DOCTOR OF PHILOSOPHY
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BY

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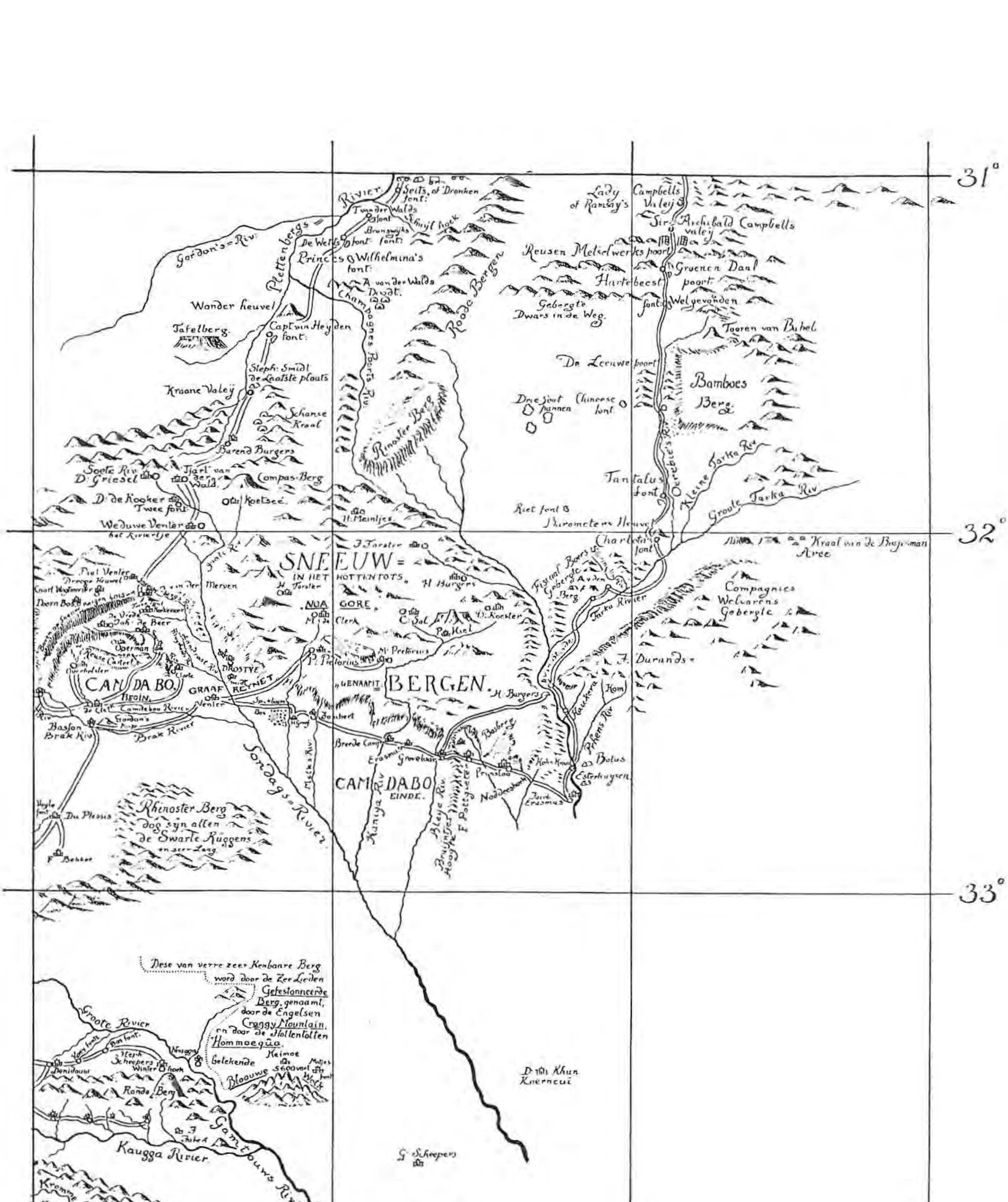

THE EASTERN CAPE 1777-87
drawn by Colonel R J Gordon.
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Frontispiece

ABSTRACT

An hierarchical syntaxonomic classification of the vegetation of the Camdebo and Sneeuberg regions of the karoo biome is presented as a second approximation after the earlier work by Acocks (1953). Details on the geomorphology, geology, climate, and early vegetation history of the area are given. The vegetation of the study area was stratified with the aid of Landsat imagery and the community classification was generated using two-way indicator species analysis (Twinspan) which produced ordered phytosociological tables. Tabular comparisons and final sorting of tables are according to the methods and techniques of the Zürich-Montpellier school of phytosociology. Syntaxonomic ranks are defined as five classes, nine orders and seventeen communities. The classes are Grasslands, Karoo Shrublands, Karoo Dwarf Shrublands, Sub-tropical Transitional Thicket, and Riparian Thicket. The distribution of syntaxa corresponds with the steep precipitation gradient experienced in the study area.

These vegetation concepts are applied to the description of the flora of the Karoo Nature Reserve and an analysis of the total flora of the reserve is provided. The communities of the pediments, which contain the highest number of endemics, are poorly conserved. I test the validity of the vegetation classification by interpreting the results of an analysis of soils within the hypothesized vegetation units. There is a gradient of increasing Na, silt and pH levels from the Shrublands and Grasslands to the Succulent and Grassy Dwarf Shrublands of the pediments.

A qualitative model of the vegetation history during the glacial-interglacial sequence in the Graaff-Reinet region of the eastern Cape is presented. Using a descriptive approach, the distribution patterns of 68 taxa, which are differential species for Karoo Shrublands, Succulent Thicket and Karoo Dwarf Shrublands, are investigated relative to major southern African biomes. The results indicate that a large proportion of the differential species in the phytosociological classification show affinity with Grassland and Savanna Biomes. Three species groups encountered in the Dwarf Shrublands show affinity with the Nama-Karoo biome. The differential species of the Succulent Thicket have a predominantly subtropical distribution. Using an historical approach, the palaeoenvironment of the region during the past 20 000 years is discussed briefly. On the basis of the descriptive and historical perspectives, a qualitative model of vegetation history is presented.

The Succulent Thicket may have become established on edaphically favourable sites in the ameliorating conditions of the warmer, wetter Holocene subsequent to the Last Glacial

Maximum. The Dwarf Shrubland and Succulent Dwarf Shrubland are depauperate in relation to communities in other southern African biomes, but the relatively large number of endemics suggests a long history in the region. Their differential species groups occur under arid conditions, accompanied by soils with high base and fertility status. The Dwarf Shrublands may have been more extensive during the drier glacial times on those sites currently occupied by Shrubland. The Shrublands display the expected affinity with the Grassland and Savanna Biomes. The small number of endemics suggest that these communities may have occupied the region in the period since the Last Glacial Maximum. Species with Succulent Karoo Biome affinity are poorly represented.

The reliability of using Landsat products to detect and map the vegetation of the region is assessed. The manual classification of Landsat standard products provides a poor reflection of the vegetation of the arid, sparsely-vegetated bottomlands and pediments. The products provide good representation of the boundaries of thicket vegetation, but this uni-temporal approach does not distinguish between floristically different thicket communities. After analyzing digital Landsat data, I suggest that the multi-spectral scanner detects the boundaries of broad soil pedons and geological formations in areas of low vegetative cover.

I describe and map the vegetation categories of the region after manual interpretation of six Landsat scenes. This is an efficient, cost-effective method of mapping vegetation in extensive regions. The mapping units do not reflect the syntaxonomic classification, representing rather an integration of physiographic, pedological, geological and floristic information. With the view to improving the classification of these units, I develop a qualitative model of the natural resources of the region using an expert system.

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DEDICATION

I dedicate this work to my parents, Ted and Hilda, who provided me, at great cost to themselves, with the opportunity to embark on a career in the natural sciences. Their interest, concern and love for all living things had a lasting influence on me and for this I am profoundly grateful.

ACKNOWLEDGEMENTS

Throughout this study I have received support and encouragement from my wife Carolyn, and my children Richard and Nicola. During the years of field work, when Richard and Nicola were much younger, Carolyn spent many weeks caring for them on her own. In the final effort she has provided me with enormous emotional support. For these contributions I am deeply grateful.

Roy Lubke has been a colleague and supervisor, providing constructive criticism and encouragement. His door has always been open, and I look forward to further co-operative effort.

To the staff of the Chief-Directorate, Nature and Environmental Conservation in the eastern Cape, I wish to express my thanks. These colleagues provided support, particularly Dan van Schoor, Ken Coetzee, Peter Burdett, Cedric Newton, Rory Allardice and Graeme Munro. During part of the study, Rosemary Harrison provided me with able assistance. Brian Wilmot, and the staff of the Albany Museum, have provided the stimulating environment in which to proceed with this research.

I have received inspiring support from farmers in the region, particularly the McCabe's of St. Olives, the Herold's of Ordonantie and Brooklyn, and the Trollip's of Compassberg. To my colleagues on the Karoo Biome Programme, I extend sincere thanks. The injection of ideas that the programme provides have contributed immeasurably to this project. Richard Cowling, Timm Hoffman, Peter Novellie, Annelise le Roux and Wendy Lloyd need special mention for the critical discussion which they have provided.

I wish to extend my appreciation to the Director, Botanical Research Institute for allowing me to continue this research. Estelle Brink, Dr Amy Jacot-Guillarmod, Chris van Ginkel and Alfred Booi, from the Botanical Research Unit, Grahamstown, assisted with identifications, prepared diagrams and maps, and provided distribution details. Chris Scheepers accepted me into the Vegetation Ecology Division during a demanding phase in this project, and has provided me with financial and moral support.

I wish to thank the Chief-Director, Department of Nature and Environmental Conservation, for providing funding from 1979 to 1986. The Co-ordinator of the FRD's National Programme for Remote Sensing provided support for Miss RMG Harrison, under the section Land Cover (Vegetation). The Department of Agriculture and Water Supply, through the Botanical Research Institute, has supported the project under Facet Technical Number PL 125/27/2/1.

PREFACE

I initiated this project at a time when there was a need for synthetic descriptive research on the vegetation of the Karoo. The Dwarf Shrubland was being called "bossieveld" and there had been little attempt to further develop the earlier work of JPH Acocks. I wished to prepare a vegetation classification system which would have some appeal to the land-user. Changes in Karoo vegetation are viewed as a consequence of recent anthropogenic influence. It was my intention to assess and discuss these views using the results of indirect gradient analysis.

Throughout my studies in the Karoo, I have been inspired by the efforts of Richard Cowling at providing a refreshing approach to the synthesis of regional vegetation. His writings, as Co-ordinator of the Karoo Biome Programme, and his publications on the vegetation of the Humansdorp region of the fynbos biome, have provided models for this, and other, synecological accounts of the vegetation of southern Africa. Primarily I have been inspired by the writings of JPH Acocks, who single-handedly completed the vegetation map of South Africa (the equivalent of thirty 1:250 000 Topo Series Sheets) in less time than it has taken me to complete two sheets, without the availability of satellite imagery. Throughout this study I have marvelled at the accuracy of his mapping, and the well formulated concepts of the vegetation hierarchy which he developed. JPH Acocks and CEM Tidmarsh left a small following of converts in the Camdebo and Sneeuberg regions, and from these farmers I have received many insights into the dynamics of the vegetation. They represent a small community who have carried out the long-term experimentation which Acocks and Tidmarsh proposed, repeating the decision making in an objective manner over twenty five years. Their "experiments" provide further examples of the categories of "treatment" which the Karoo is experiencing.

While investigating the recent history of the study area, I studied a map from the collection of Col. R.J. Gordon (frontispiece). On that map, the land from 32° to 33° S and from 24° to 26° E is called the "Sneeuwbergen" and "Camdabo". As this includes most of the study area, I use the historical names Camdebo and Sneeuberg to describe the area encompassed by these co-ordinates. Other large mountain ranges and plains within the study area include the Bankberg, Boschberg, Aberdeen Plain and the Noorsveld.

GENERAL INTRODUCTION

The Karoo-Namib region (Werger 1978, White 1978) is one of the largest single areas of natural vegetation in southern Africa, comprising the Nama-Karoo, Succulent Karoo and Desert biomes (Rutherford & Westfall 1986). This study concerns the proposed Nama-Karoo biome, which covers 541 000 km^2. The extent of the region, together with its economic importance for fleece production, make it imperative that an understanding of the ecological limitations of the system should be determined. Initially the vegetation appears to be transformed, but the numerous ungulate populations appear to have survived throughout, with relict populations being found on newly established nature reserves in the region. The short period of European occupation and farming in the Karoo has provided only limited knowledge, gained by experience, about the functioning of the system. I have been struck throughout my studies in the eastern part of the biome by the paucity of substantiated evidence for a trend in the direction of vegetation change, be it anthropogenically- or climatically-induced. The frequency of drought, accompanied by the flat, monotonous terrain, evokes a negative impression in western man. These features have probably exacerbated and perpetuated the attitude in agricultural planning that the present vegetation of the Karoo is largely the consequence of excessive utilization of the vegetation by domestic ungulates (principally cattle and sheep). The initiation of these attitudes can be traced back to the literature after the formation of the Union of South Africa, and the subsequent establishment of the Drought Commission. It may have been politically expedient at that time to encourage land-owners to stay on the land, irrespective of the potential of the natural vegetation to support livestock on a continuous basis. This could further have aggravated the interaction between the land-user and the resource.

My interest in the vegetation of the Karoo was stimulated by the response which the vegetation of the eastern Cape has to varying land-use "treatments". I use the term "treatment" in a broad context, referring to the numerous land-use categories which have been developed in the region, including intensive and extensive pastoral agriculture, nature reserves and national parks, game farms, agricultural research stations, undemarcated state land withdrawn from agricultural use, road and rail reserves, outspans, town commonage and inaccessible mountain plateaux. To this list can be added many more categories, each providing a perspective into the response which the vegetation may have to use, or lack thereof, by wild and domestic ungulates. Human activity in the Karoo has divided the landscape up into a multiplicity of units, and seldom has it been possible to interpret the cause and effect relationships between the vegetation and its environment. As a first step towards initiating some well-formulated hypotheses for testing, I became interested in classifying the vegetation of a 41921 km^2 section of the region. It has been suggested that mapping rangeland would be facilitated by using satellite imagery (Cihlar & Thompson 1978), especially Landsat MSS data with its high spatial resolution. I tested these products before proceeding with extensive mapping. During the reconnaissance I prepared a second approximation of the Acocks (1975) Veld Type map using Landsat MSS data.

Nature reserves have been established in the region in an effort to preserve the biotic components within discrete boundaries. In semi-arid ecosystems, the ecosystem processes are inter-connected to such an extent that a small nature reserve cannot be viewed as an isolated land parcel enjoying some special status. This is particularly true in the Karoo where a multiplicity of biotic consumers transgress the barriers around reserves, and the export and import of nutrients to and from the system during episodic events may be great. I refer to the movement of wild ungulates, birds, small mammals and invertebrates across and through artificial barriers. The geomorphological processes operating in the Karoo result in the transport of nutrients and moisture from the mountains to the pediments and bottomlands, but the importance of these processes to ecosystem function are poorly understood.

The eastern Cape is a "tension zone" for the vegetation of the sub-continent, with floristic elements from five phytochoria meeting here. The Camdebo and Sneeuberg regions reflect part of this complex phytochorology, providing an opportunity to tentatively test some of the theory on the origin of the flora. I wished to assess the phytochorological affinity of selected species using an objective method, and together with a review of palaeoclimatic data, present a model of regional vegetation history.

Further analysis of the total floristic list from the Karoo Nature Reserve provides some insight into the inadequacy of formal conservation of the Karoo flora. This assessment is mitigated by the enormous contribution being made by the many private land-owners who protect and manage the natural vegetation in an exemplary fashion.

It is my intention to submit the manuscripts in this thesis for publication and I have followed the editorial style of the journals in which I wish to publish.

This investigation of the vegetation of the study area has involved the formulation and testing of a number of hypotheses, in order to establish a set of working hypotheses for the region. The hypotheses have been in two fields of research: the vegetation/environment interaction and the detection of this vegetation using remote sensing. I divide this thesis into two parts, representing these two research fields. The results of the two parts are integrated in the general discussion.

PART I

I develop a vegetation description for the Camdebo and Sneeuberg region using the results of a phytosociological survey. The regional vegetation consists of Shrublands and Grasslands of the cool, dry mountainous terrain; Grasslands of the cool, wet slopes and pediments; Dwarf Shrublands, Grassy Dwarf Shrublands and Succulent Dwarf Shrublands of the hot, dry pediments; Succulent Thicket of the hot, dry, upper pediments; and the Riparian Thicket of the bottomlands.

These vegetation concepts are applied to the description of the flora of the Karoo Nature reserve and an analysis of the total flora of the reserve is provided. The communities of the pediments, which contain the highest number of endemics, are poorly conserved in the region. I test the validity of the vegetation classification by interpreting the results of an analysis of soils within the hypothesized vegetation units. There is a gradient of increasing Na, silt and pH levels from the Shrublands and Grasslands to the Succulent and Grassy Dwarf Shrublands of the pediments.

A qualitative model of the vegetation history of the region is prepared using the results of the descriptive study. This model is tested using perspectives of the palaeoclimate and analysis of the levels of endemism.

A syntaxonomic and synecological account of the Camdebo and Sneeuberg regions of the karoo biome.

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Abstract

An hierarchical syntaxonomic classification of the vegetation of the Camdebo and Sneeuberg regions of the karoo biome is presented as a second approximation after the earlier work by Acocks (1953). Details on the geomorphology, geology, climate, and early vegetation history of the area are given to provide the setting for this and other papers dealing with the floristics, community differentiation, plant/soil relationships, mapping and phytogeography. The vegetation of the study area was stratified with the aid of Landsat imagery and the community classification was generated using two-way indicator species analysis (Twinspan) which produced ordered phytosociological tables. Tabular comparisons and final sorting of tables are according to the methods and techniques of the Zürich-Montpellier school of phytosociology. Syntaxonomic ranks are defined as five classes, nine orders and seventeen communities. The classes are Grasslands (2 orders, 3 communities), Karoo Shrublands (1 order, 5 communities), Karoo Dwarf Shrublands (4 orders, 5 communities) and Sub-tropical Transitional Thicket (1 order, 3 communities), with one community representing the Riparian Thicket. Discussion of the scheme focuses on the level of the order (*sensu lato* veld type). In addition to diagnostic floristic elements, syntaxa are further characterized using structural and habitat criteria. The distribution of the syntaxa displays a correspondence with the steep precipitation gradient experienced in the study area. Succulent Dwarf Shrublands occur in areas of low mean annual precipitation (<250 mm) on minerally-rich brack (saline) soils. Grassy Dwarf Shrublands occur in areas receiving 250-350 mm per annum on calcium rich soils. The Shrublands occur on steeply sloping landforms with higher precipitation (350-450 mm), with Grasslands receiving >450 mm per annum. The Succulent Thicket occupies warm, dry sites on rocky, sloping landforms.

Uittreksel

'n Hiërarchiese sintaksonomiese klassifikasie van die plantegroei van die Camdebo- en Sneeuberg-streke van die karoo bioom word weergegee as 'n tweede benadering op die vorige werk van Acocks (1953). Inligting oor die geomorfologie, geologie, klimaat and vroër plantegroei geskiedenis van die gebied word gegee om die setting vir hierdie en ander referate oor die spesiessamestelling, gemeenskap differensiasie, grond/plant verhoudinge, kaarteering and fitogeografie. Die area is deur middel van Landsat beelde gestratifiseer en die gemeenskap klassifikasie is met behulp van twee-rigting indikatoor spesies analise (Twinspan), wat fitososiologiese tabelle produseer, voorberei. Vergelyking en finale sorteering van tabelle is volgens die metodiek en tegnieke van die Zürich-Montpellier skool van fitsosiologie onderneem. Sintaksonomiese range word as vyf klasse, nege orders en sewentien gemeenskappe gedefineer. Die klasse is Grasveld (2 orders, 3 gemeenskappe), Karoo Struikveld (1 order, 5 gemeenskappe), Karoo Dwerg Struikveld (4 orders, 5 gemeenskappe) en Sub-tropiese Oorgangswoud (1 order, 3 gemeenskappe). Bespreeking van die skema vind plaas op die vlak van order (*sensu lato* veld tipe). Sintaksa word verder gekarakteriseer met behulp van strukturele en habitat kriteria, sowel as diagnostiese floristiese elemente. Die verspreiding van die sintakse korrespondeer met die skerp reënval gradient wat in die studie gebiede ondervind word. Sukkulente dwerg struikveld kom in gebiede voor wat laë jaarlikse reënval (minder as 250 mm) op mineraal-ryk, soutagtige grond voor. Grasagtige dwerg struikveld kom in gebiede wat 250-350 mm per jaar ontvang, op kalsium-ryk grond, voor. Die struikveld kom op styl landvorms met hoër reënval (350-450 mm) voor, met grasveld in gebiede wat >450 mm ontvang. Die oorgangswoud kom meestal op warm, droë plekke op daelende landvorms voor.

INTRODUCTION

The karoo biome (Cowling 1986) was the domain of the late JPH Acocks who spent thirty one years stationed at the Agricultural Research Institute for the Karoo Region, Middelburg, Cape Province. In his standard guide for most vegetation work in southern Africa (Acocks 1953, 1975) Acocks presents a concept of the veld type as an "agro-ecological unit of vegetation" (Cowling 1984). He had, according to Cowling (1984), "a brilliant perceptive overview of vegetation patterns in South Africa". Acocks (1953) completed this work at a time when the assumptions of Clementsian dynamics were largely accepted. The subjective techniques Acocks used precluded a clear definition of "veld type" and he incorporated "structurally and floristically unrelated types into a single veld type" (Cowling 1984). In this paper I present a syntaxonomic hierarchy of vegetation units as a second approximation to the work of Acocks, focusing on the level of order. I use floristic and structural criteria to describe syntaxa and to prepare testable hypotheses regarding their origins and interrelationships. In addition, I expand on the physical environment of the study area, and provide the setting for further papers on the floristics and community characterization of the Karoo Nature Reserve (Palmer 1988a & b); plant/soil interactions in the Camdebo and Sneeuberg regions (Palmer 1988c); an assessment of the reliability of using Landsat false colour imagery to map the vegetation (Palmer 1988d, Palmer 1988e); and phytogeography (Palmer 1988f).

The natural vegetation of the Karoo Region is a resource which supports a substantial export industry for the Republic of South Africa, with the 1985 fibre production from sheep and goats alone in the region having an export value of approximately R 586,6 million (Anon. 1987), equivalent to 24,6% of total agricultural export. This industry is almost exclusively dependent on the production of the natural veld, and its continued growth is linked to an improved understanding of the resource base.

Researchers in the semi-arid regions of southern Africa ascribe the apparent accelerated desertification to mismanagement of domestic herbivores, especially sheep (Marloth 1908, De Klerk 1947, Acocks 1964, Werger 1980). The possibility of increased desertification was raised by the Drought Investigation Commission (Anon. 1923) and has subsequently been elaborated on by various authors (Potts & Tidmarsh 1937, Tidmarsh 1948, van der Merwe *et al.* 1951, Acocks 1953, 1964, 1979, Roux 1980). This literature fails to present any long-term data sets as corroborative evidence. The circumstantial evidence from proxy historical data (Roux & Theron 1987) does little more than raise further questions.

The study was undertaken in the eastern Cape midlands, towards the eastern limit of the Nama-Karoo biome (Rutherford & Westfall 1986) in an area that provides a microcosm of four biomes (Palmer 1988f). It was appropriate to study the vegetation of an area where steep gradients in topography and climate are encountered as these gradients provide an opportunity to follow changes in the environment, and the concomitant change in vegetation floristics and structure.

1.0 THE STUDY AREA

The study area (Figure 1) extends from 32° to 33° S and 24° to 26° E and includes the Camdebo (spelling according to Raper 1987) and Aberdeen plains, and the mountains of the Great Escarpment (King 1942), including the Winterhoekberge and Sneeuberge and comprises 1:250 000 SA Topo Series sheet, 3224 Graaff-Reinet. The area, covering some 20000 km^2, contains thirteen of Acocks' sixty veld types (Palmer 1986) and can be divided into three units, namely the southern plains, the mountain ranges and the northern plains. The Camdebo and Aberdeen plains are large interior basins which overlie resistant rocks, upon which deep, alluvial soils have been deposited or developed *in situ* (Johnson & Keyser 1976).

The mountains within the region contain dolerites which have been forced through the older Karoo sedimentary rocks. Subsequent erosion of weaknesses in the dolerites have resulted in

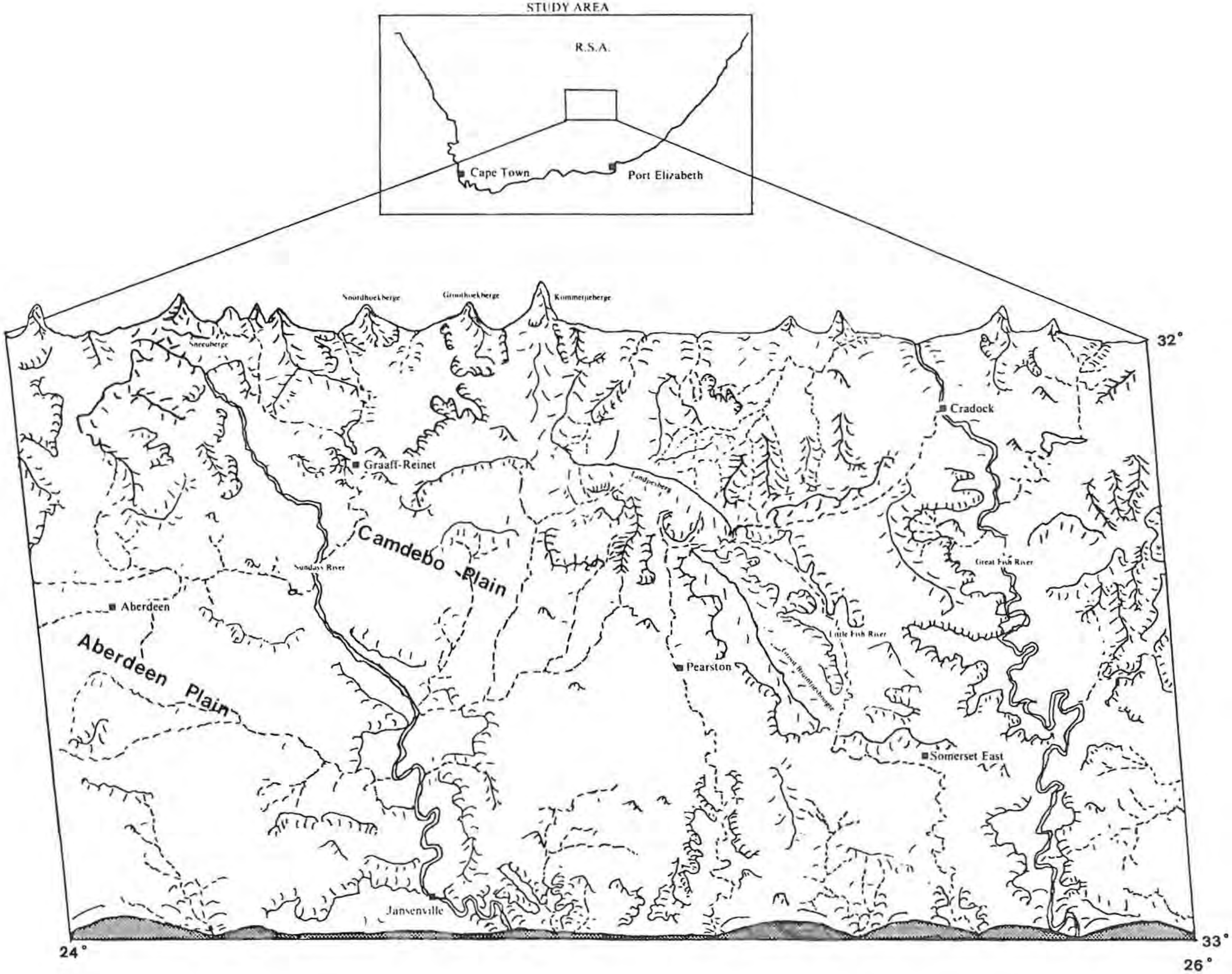


Figure 1. The study area, showing the Camdebo and Aberdeen plains, and the mountains of the Great Escarpment.

the characteristic landscape of buttes and mesas. The dominating feature of the mountainous landscape is the Nadouwsberg Peak (2416m), which is the highest peak of the Tandjiesberg range. Other ranges are, from west to east, the Koueveldberge, Sneeuberge, Bankberg, Coetzeesberge, Agter-Bruintjieshoogte and Groot Bruintjieshoogte. These mountains form the boundary between the Camdebo plains and the high altitude interior. The mountains extend from east to west in the northern parts of the study area, finally veering in a south-easterly direction towards Somerset East. The study area comprises a large proportion of the upper catchment of the Sundays and Great Fish rivers.

GEOMORPHOLOGY

The rock terraces, mesas, buttes and needles (Hobbs 1923) are characteristic profiles of arid landscapes. These geomorphological components have their origins in the geological activities which characterize the geological history. The macro-scale landscape extends from the Great Karoo, across the mountains of the Great Escarpment to the Upper Karoo (King 1942), referred to by Kruger (1983) as the Southern Interior Basin. The meso-scale landforms can be described using a broad catenary arrangement of land facets in a ten class system (Scheepers 1987). These can be summarized as plateaux, plains, rugged peaks, upper pediments, middle pediments, lower pediments, bottomlands, levees, gullies and drainage lines. Further description of the surface features follows Gabriel & Talbot (1984) and Harmse *et al.* (1984). Landform establishes a moisture gradient (Knight 1987) which is an important abiotic determinant of plant cover in semi-arid regions (Shmida 1985).

The large basins found between the dolerite dykes form the distinctive Karoo *vlaktes* or pediments. The areas are never completely flat, and are generally traversed by a drainage line, or an erosion gully or donga. The donga is a short-term erosion gully, typically steep-sided (Scheepers 1987) in the deep structureless alluvium deposited in the Quaternary period. Dongas may be up to 10 m deep, with resistant bedrock (usually blue-grey mudstone of the Adelaide Subgroup) preventing further downward movement.

The pediments contain features such as the "brak-kol" or shallow pan where sodium, calcium and magnesium carbonates have accumulated. Gabriel & Talbot (1984) describe a "pan" as a horizontal layering of soil that is compacted, and through which the movement of water and the growth of roots is impeded. This layer, described as a hardpan calcrete or dorbank (Mac Vicar *et al.* 1977) is extremely hard and permeable, allowing water to percolate through, but inhibiting the passage of the roots of all but the most adapted plant species.

Erosion of the soil surface by wind and water is an important phenomenon in the karoo biome (Walters 1955, Opperman & Roux 1986) and it has been suggested that soil capping, and erosion of the A-horizon results in a poor germination environment for indigenous plant species. Wind erosion is a significant disturbance factor (Walters 1955) as any light organic material is transported away from the site before it can be incorporated into the A-horizon. The strength and duration of wind (Figure 2) contributes to the maintenance of aridity in the region, and its influence warrants investigation.

GEOLOGY

The oldest rocks in the region are the grey and "red" mudstones and sandstones of the Middelton formation (Adelaide Subgroup of the Beaufort Group: Karoo Supergroup). These are sedimentary rocks of Upper Permian age (Johnson & Keyser 1976) and contain vertebrate fossils of *Cistecephalus* and *Daptocephalus* Assemblage and Zones. The anomodont reptile *Oudenodon baini* Owen is fairly common throughout the succession.

The Adelaide Subgroup consists of alternating layers, a few metres to a few tens of metres thick of grey, fine-grained sandstone (25%) and greenish-grey, bluish-grey or greyish-red mudstone (70%). The sandstones show horizontal lamination ("flat-bedding") and the mudstones are poorly stratified or massive (Johnson & Keyser 1976). The top of the Adelaide subgroup can be defined as a horizon above which sandstone predominates over mudstone. The Tarkastad subgroups consists of the Katberg Sandstone formation and the Burgersdorp formation. In the former, the sandstones comprise 90-95% of the total thickness, with greyish-red and sub-ordinate greenish-grey mudstone constituting the remainder. The latter group consists of light greenish-grey, olive-grey, or brownish-grey, fine-grained sandstone (30%), and greyish-red with subordinate greenish-grey mudstone (70%). In the eastern section of the study area lie the fossiliferous beds of the Katberg formation (Tarkastad Subgroup of the Beaufort Group). These beds may be up to 500 m thick and mudstone constitutes about 30% of the formation (Johnson & Keyser 1976).

The sedimentary rocks of Permian to Triassic age have been intruded by numerous dykes, sills and inclined sheets of Jurassic-age dolerite (Figure 3). Dolerite is the common basaltic rock which cooled quickly from lava flows, giving rise to coarse-grained volcanic rock forming dykes and sills (Holmes 1965). These dolerite intrusions were forced through the sedimentary Beaufort beds and deposited on the surface. Crustal activity initiated erosion cycles which exposed the underlying Beaufort Group. Relics of these formations are the numerous narrow ridges (dykes) which traverse the area, and the massive granites which

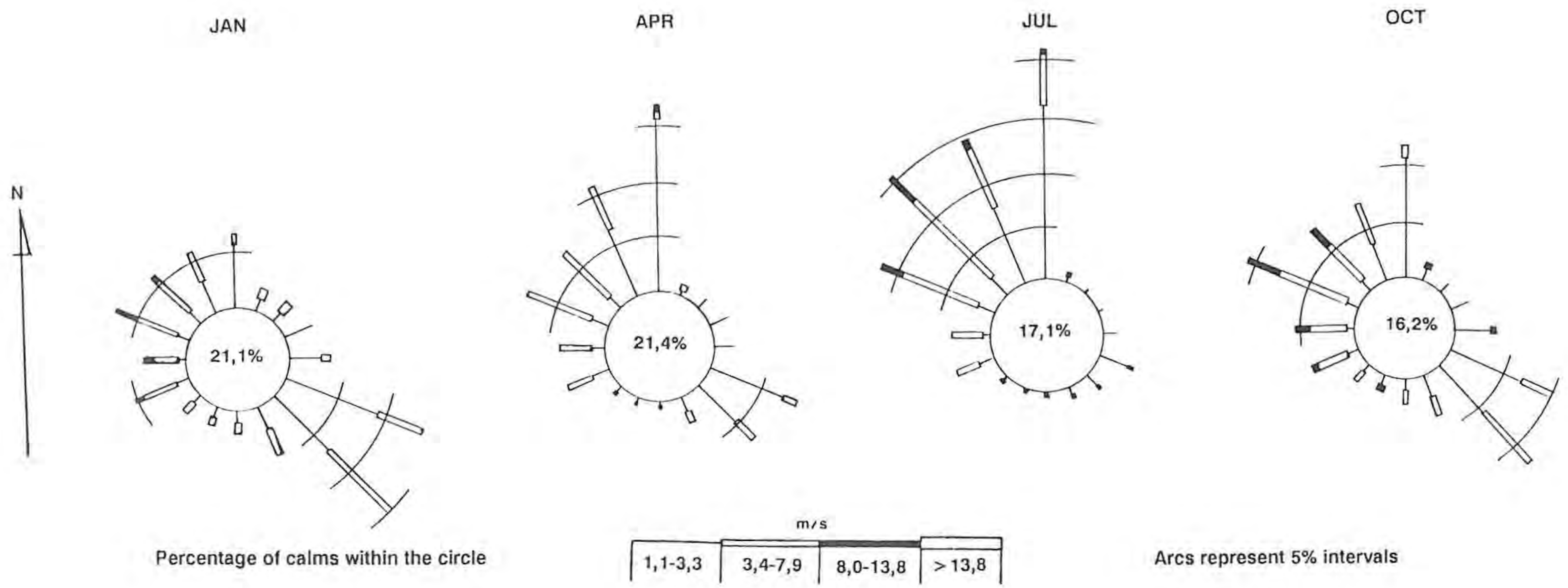


Figure 2. Windroses for Middelburg, Cape.

LEGEND

Trt	Mudstone sandstone	Tarkastad Subgroup	Beaufort Group	KAROO SUPERGROUP
Pa	Mudstone sandstone	Adelaide Subgroup	Beaufort Group	KAROO SUPERGROUP
Pwa	Sandstone shale	Waterford Formation	Beaufort Group	KAROO SUPERGROUP
Pf	Shale	Fort Brown Formation	Ecca Group	KAROO SUPERGROUP
Pr	Sandstone shale	Ripon Formation	Ecca Group	KAROO SUPERGROUP
Jd	Jurassic Dolerite			

3224 Graaff-Reinet

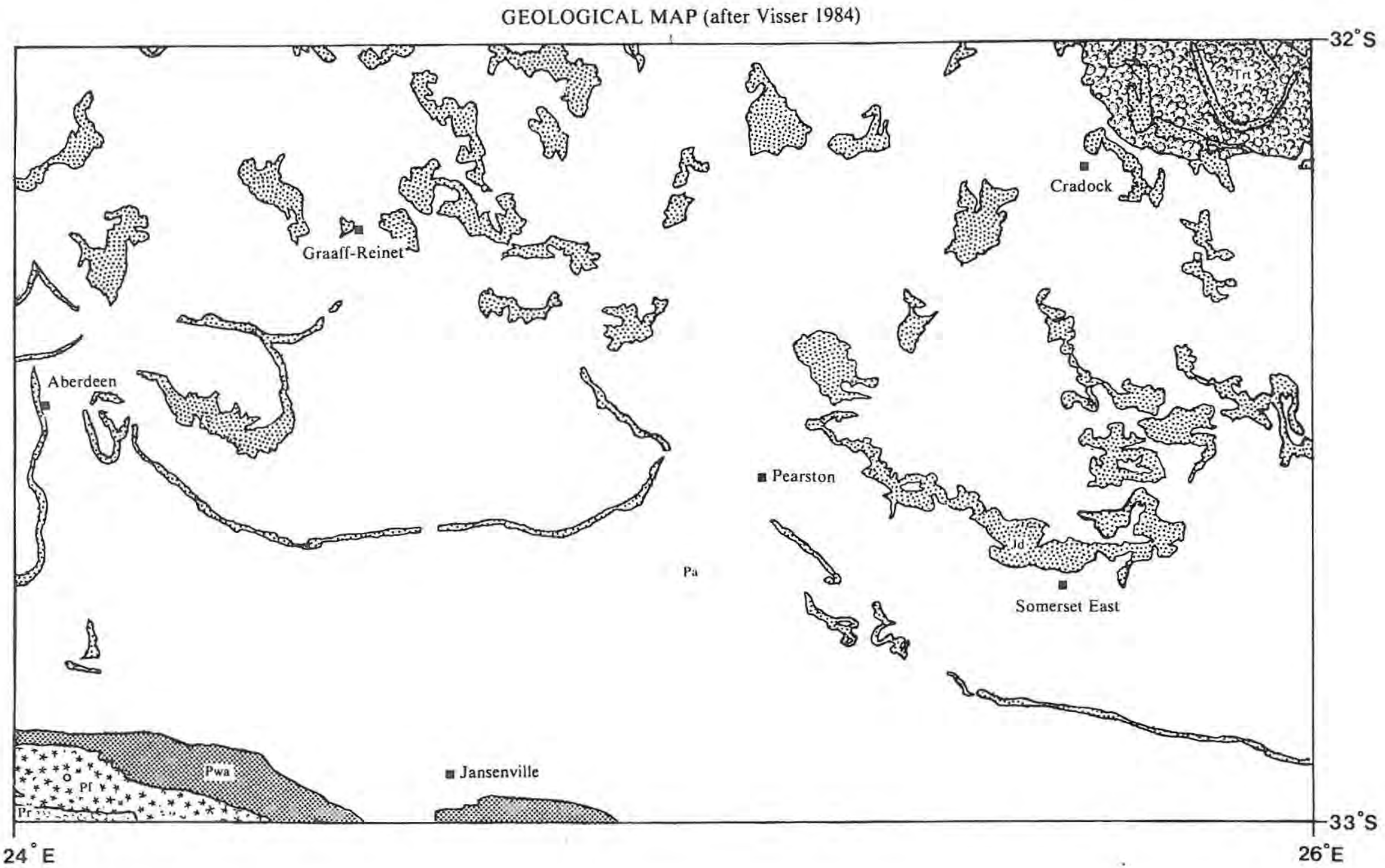


Figure 3. The geological map (after Visser, 1984).

underlie large mountains (e.g. Rooiberg). Horizontal layers of dolerite cap the sediments and erosion has resulted in characteristic topography such as Spitzkop and Spandaukop. Another striking feature is the concentric pattern formed by many of the dolerite intrusions (Johnson & Keyser 1976). Erosion of the dolerite dykes influences the geology of the underlying sandstones and mudstones.

Quaternary sediments are encountered in two forms in the inland basin, namely alluvial deposits formed on the flood plains of major watercourses; and colluvial deposits which are thin but extensive surface deposits formed by sheetwash.

CLIMATE

Historical climate

"The climatic history of southern Africa has been characterized by great change and variability" (Tyson 1986). For example, at the time of the last glacial maximum (18000 BP - most precise date Talma & Vogel, 1986), although glacial conditions were never experienced, periglacial conditions prevailed at high elevations.

From 16000 to 10000 BP conditions may have been wetter and cooler than at present (Scholtz 1986, Deacon & Lancaster 1988). However, Meadows *et al.* (1987) present palaenological evidence from a site in the Winterberg (100 km east of the study area) to suggest that there have been no obvious trends in the climate since 8000 BP.

The journals of Le Vaillant (1796) and Barrow (1801), and evidence from enhanced growth phases in tree-ring series (Tyson 1986), indicate that the interior of southern Africa may have been wetter during the late eighteenth and early nineteenth century than at present.

Some of the oldest meteorological stations in southern Africa are located in the karoo, with rainfall records from Graaff-Reinet beginning in 1861 and Grahamstown in 1865. Tyson (1986) rejects the hypothesis that southern Africa has undergone progressive desiccation during the period of the meteorological record. Oscillatory variations in the rainfall are much more apparent. Tyson (1986) showed that a series from 157 stations in the north-eastern summer rainfall region over the period 1910-1972 exhibited a surprising degree of temporal variation. Spectral analysis offers an independent means of detecting rainfall oscillations. The rainfall spectra for Graaff-Reinet and Grahamstown display regular temporal variation in annual rainfall (Figure 4) (Tyson 1986).

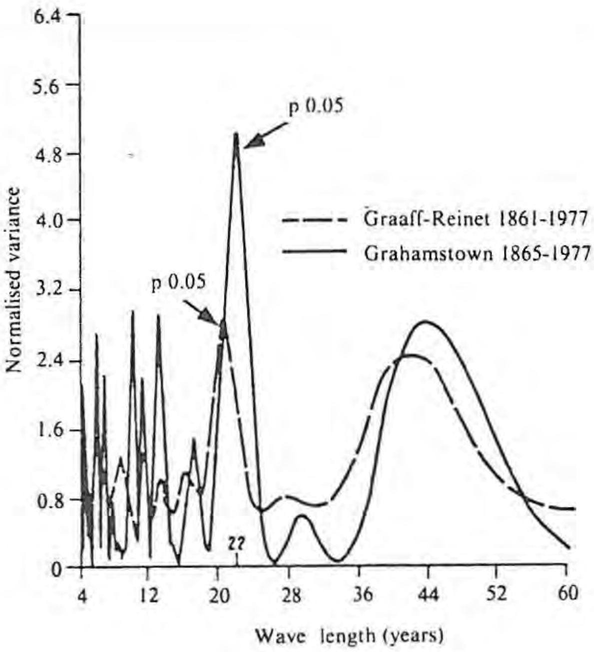


Figure 4. Rainfall spectra for Graaff-Reinet and Grahamstown, displaying remarkably reliable temporal variation in annual rainfall in a 22 year oscillation (after Tyson, 1986).

Present climate

The mean annual rainfall of recording stations in the study area ranges from 284mm at Aberdeen to 591mm at Somerset East. The climate diagrams (Walther & Lieth 1960), prepared for stations with known temperature data (Figure 5), show steep rainfall gradients. The reliability of rainfall diminishes from west to east (Venter *et al.* 1986) with 60-70% of the mean annual rainfall falling in summer (October to March). The isotherms of Venter *et al.* (1986) present mean annual temperatures from 15 to 17,5 °C, with summer (January) maximum temperatures ranging from 30-32°C and 10-20 days per annum with minimum temperatures below 0°C. A cool steppe climate (Schulze 1947) is experienced by the mountains of the Great Escarpment, with a warm steppe climate in the eastern lowlands (Vorster 1985). The rainfall conditions of much of the study area correspond with Shmida's (1985) definition of a semi-desert or semi-arid ecosystem (150-300 or 400 mm per annum).

GENERAL

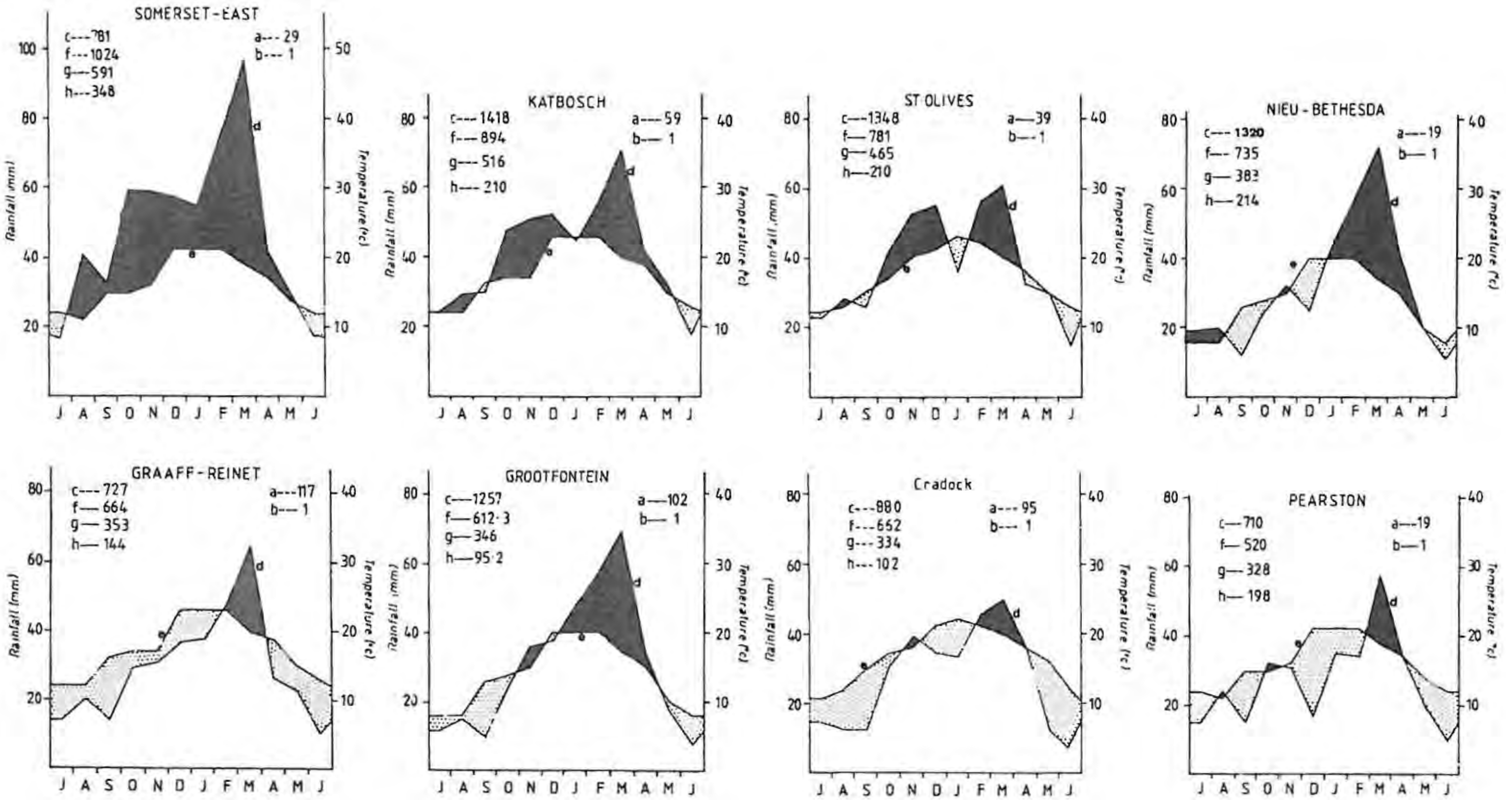
Early vegetation history

One of the earliest references in the natural history literature to the vegetation of the semi-arid interior of southern Africa is that of Thunberg (1793) who mentions that in 1771, while travelling in the country behind the Swartberg range, the:

> "plants as well herbs as bushes, stand very thin in the Carrow-veld; and, in such a burning hot climate, where not drop of rain falls for the space of eight months at least, it is almost inconceivable how they can thrive at all. Their stems and branches likewise have the appearance of being brittle and quite dried up; but the leaves, on the other hand, are very thick and filled with briny fluid, and remain green all year through."

Skead (1988) comments that historical travellers were seldom complimentary about the flat stretches of veld encountered in the region. Sparrman (1786) after his travels in 1776 mentions that the Camdebo " is an arid, flat, Carrow-like country inhabited by Christians who are chiefly employed in cattle rearing". This gives some hint of the grassiness of the vegetation which Sparrman encountered. Francois Le Vaillant (1796) describes the area from Pearston flats to the Voëlrivier as being covered with "coarse grass and weeds, with only small tufts of grass". These were amongst the first explorers to describe the conditions in the Camdebo, and to use the name "karoo", which is derived from the KhoiSan word "Kuru" meaning dry, or harsh (Nienaber & Raper 1977).

Skead (1988) notes that John Barrow (1801) travelled from Graaff-Reinet to Jansenville in August 1797 and wrote: "Our first route lay directly to the southward... through a country as



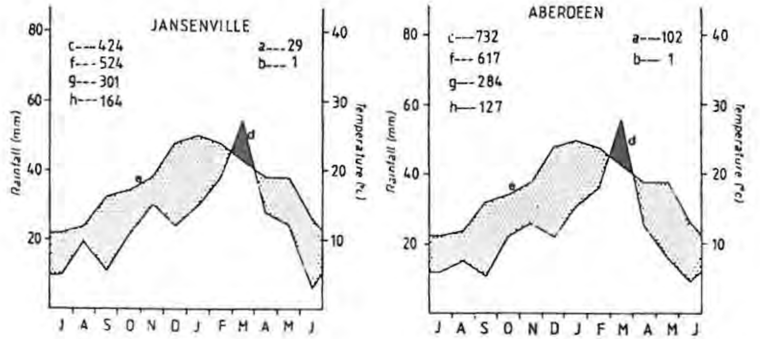


Figure 5. Climate diagrams for recording stations in the study area.

LEGEND. (a) Number of recording years (rainfall); (b) Number of recording years (temperature); (c) Altitude; (d) Curve of mean monthly rainfall; (e) Curve of mean monthly temperature; (f) Highest annual precipitation (mm); (g) Mean annual precipitation (mm); (h) Lowest annual precipitation (mm) sandy, arid, and sterile as any part of the Great (Karoo) Desert." This description suggests that the vegetation oscillated between dwarf shrubs and grass depending on the quantity of rain during the previous season.

Bolus (1875) suggested the karoo is a distinct phytogeographical unit, distinguishing it from that of the Kalahari and the Namib. Marloth (1908) defined the vegetation of the region according to the presence of seven growth-forms, namely **bushes** and **dwarf shrubs, leaf succulents, stem succulents, plants with underground water storage, bulbous monocotyledons, grasses and annuals**. He referred to the most typical example of karoo vegetation as Gouph or Goup (Raper 1987) a Khoisan word said to mean "fat" referring either to succulent vegetation or well fed stock. Bews (1916) described the "Karroo" as a **succulent sclerophyllous dwarf shrub** type which is the product of a dry, continental climate on grassland.

In his description of the vegetation map of South Africa, Pole-Evans (1936) refers to the "Karoo" as part of the "**Desert shrub**", but makes no mention of it being a vegetation type of its own. Dyer (1937) suggests the term "**karroid scrub**" to describe the vegetation type which occurs in the Albany district of the eastern Cape. The term "Karroo" is a general one and cannot be "applied to any geographical region and still less to any one type of vegetation" (Adamson 1938). Two types of "Karroo" vegetation were distinguished by Adamson (1938), namely "**Arid Bush** (Upper Karroo) and **Succulent Bush** (Great and Little Karroo)".

Acocks (1953) emphasized the karoo (the accepted spelling for the word only appeared in the literature at this time) and suggested that it was the inextricable mixing of the "Southern Fynbos (or Sclerophyll) and the forest of the winter rainfall area; with the tropical forest, savanna and grassveld of the summer rainfall area." He continued to describe units within the karoo on the basis of their floristics, and recognized twenty-two "Karoo and Karroid Veld Types" (including False Karoo and Karroid *Merxmuellera* Mountain Veld). These veld types cover 39,5 % of the total area of the Republic of South Africa (Scheepers 1983). Based on the work of Acocks (1953), Edwards (1970) prepared a generalized floristic-physiognomic map of South Africa, which described the karoo as a region occupied by **dwarf and succulent shrub**.

Martin & Noel (1960) adopted the approach of Schimper (1903), and defined the karroid vegetation which they encountered in the Albany district of the Cape Province as a "**dwarf shrub steppe formation**". Werger (1980) adopted a similar terminology in his study of the vegetation of the Orange river. The east-west aridity gradient in his study extended from grassland over **open dwarf shrub and grass** vegetation to an **open dwarf shrub steppe**. The term **steppe**, meaning chamaephyte semi-desert, is recommended (Shmida 1985) for areas dominated by dwarf shrubs. Karoo vegetation is also described as a **dwarf open shrubland** (Campbell *et al.* 1981).

With the advent of the biome approach to describing the vegetation of southern Africa, Werger (1978) and White (1983) prefer to regard the extensive arid and semi-arid areas of the south-western part of southern Africa as the Karoo-Namib biogeographical region. White (1983) divides the study area into three major vegetation types, namely **bushland and thicket, semi-desert vegetation** and **grassy shrubland.** The bushland and thicket contains one sub-division, namely **evergreen and semi-evergreen bushveld and thicket**, whereas the grassy shrubland is represented by **Karoo grassy shrubland** and **Montane karoo grassy shrubland.** The semi-desert vegetation of the study area is represented by three divisions, namely **semi-desert vegetation** in the west, **bushy Karoo-Namib shrubland** and **dwarf Karoo shrubland.** The Karoo-Namib region is divided into three biomes by Rutherford & Westfall (1986), namely Nama-Karoo Biome, Succulent Karoo Biome and Desert Biome. According to this classification, this study area falls completely within the Nama-Karoo Biome.

Biotic factors

Pastoral agriculture is the principal human activity in the study area. Large populations of sheep and goats occur, with smaller populations of cattle, horses and other domestic stock. Populations of wild ungulates, mainly springbok (*Antidorcas marsupialis*), steenbok (*Raphicerus campestris*), mountain reedbuck (*Redunca fulvorufula*), grey duiker (*Sylvicapra grimmia*), kudu (*Tragelaphus strepsiceros*) and klipspringer (*Oreotragus oreotragus*) are also present throughout the study area. Small mammals, including rock hyrax (*Procavia capensis*), springhare (*Pedestes capensis*), porcupine (*Hystrix africaeaustralis*) and numerous species of small mammals are also encountered. These species, particularly the burrowing Brant's whistling rat (*Parotomys brantsii*), ground squirrel (*Xerus inaurus*) and Karoo bushrat (*Otomys unisulcatus*), exert a constant influence on the vegetation and soil surface. Bird and insect populations also utilize the vegetation of these semi-arid areas. The recent brown locust (*Schistocerca gregaria*) outbreaks, as well as the regular harvester termite (*Hodotermes mossambicus*) and karoo caterpillar (*Loxostege frustalis*) eruptions, show that biotic influences are characteristic features of the region.

Biogeographical affinity

There is evidence of four phytochorological regions meeting in the study area. These are a

Tongaland-Pondoland succulent thicket (Moll & White 1978), Karoo-Namib elements (Werger 1978), Afro-montane remnants (White 1978), and Sudano-Zambezian grasslands (Werger & Coetzee 1978). A combination of a variable climate, complex topographical and geological patterns, and species assemblages from the phytochoria mentioned above, has resulted in complex vegetation gradients. The floristic information collected during the survey has been used (Palmer 1988f) to define the relationship between the regional flora and the biomes of Rutherford & Westfall (1986).

Previous research

Ecological studies conducted in the study area have focussed on three principle fields:

a) Studies by agricultural researchers on the relationships between grazing domestic herbivores and the vegetation (Tidmarsh 1948, 1952, 1957; Roux 1966, 1980; Roux *et al.* 1981; Skinner 1976; Vorster & Roux 1983). The trend throughout this research has been to adopt both deductive and inductive approaches.

b) Descriptive studies of the vegetation by Acocks (1953, 1975). These have been followed by semi-detailed descriptive studies by Van der Walt (1968, 1972, 1980) and Vorster (1985) of various sites within the study area.

c) Development of vegetation monitoring techniques. The early efforts of Dyer (1937), Tidmarsh & Havenga (1955) and Roux (1963) have been further developed by Vorster (1982), Novellie (undated) and Norton *et al.* (1986). The main emphasis has been on establishing permanent sites where regular collection of information is undertaken.

Individualistic versus community unit concept

The concept of classifying and mapping vegetation into units is dependent on an assumption that vegetation occurs in discrete, definable units (Clements 1916). This interpretation is also called the "community unit concept" (Whittaker 1962). The concept fails to incorporate evidence indicating that vegetation occurs along environmental gradients and represents a complex population continuum (Cain 1947, Curtis & McIntosh 1951, Whittaker 1956, 1967, 1973). The alternative concept, based primarily on the ideas of Gleason (1926, 1939), became known as the "individualistic concept" of community organization. More recently Shipley & Keddy (1987) suggest that this dichotomy is false and multiple working hypotheses of community structure should be considered. I will not attempt to elaborate further upon this debate, but have taken cognisance of the limitations of the various methods used in this study, and make mention of these limitations wherever necessary.

The community-unit concept is embodied in the classification approach of the Zürich-Montpellier School of phytosociology (Westhoff & van der Maarel 1973, Werger 1974). The concept states that vegetation consists of discrete entities which contact one another along narrow boundaries. When species' distributions are plotted along an environmental gradient or gradient-complex with a constant rate of change, groups of species or "communities" replace each other along the gradient (Whittaker 1975). The classification approach of the Zürich-Montpellier school is based on the associations which appear to exist between species occurring under similar environmental conditions.

In view of the debate surrounding the community unit concept (Shipley & Keddy 1987) it may be useful to stratify a study area using a method that is free from vegetation structure dogma. One possible solution is to determine the boundaries of the sampling units in a manner which is not directly related to the vegetation concept on the ground. In semi-arid regions the spectral reflectance attributes of the earth's surface are not strongly correlated to the vegetation of these areas (Ezra *et al* 1985, Palmer 1988d). Background geology, soil colour, soil texture and moisture influence the spectral reflectance properties more than sparse vegetation. By determining the sampling units from a manually classified false colour satellite image, I selected sample sites which were not related to a vegetation concept on the ground.

2.0 METHODS

SAMPLING STRATEGY

The methods and techniques of the Zürich-Montpellier school of phytosociology (Westhoff & van der Maarel 1973, Mueller-Dombois & Ellenberg 1974, Werger 1974, Wendelberger 1979) have been applied in this study to classify the vegetation. Sampling sites were selected using stratified random sampling (Southwood 1978). The study area was divided into individually numbered Landsat Sampling Units (LSU's) using the methods of Harrington & Dunn (1980) (Figure 6). Quadrats selected within each LSU were surveyed using the Braun-Blanquet phytosociological technique (Werger 1974). No sampling was undertaken in specialized communities (wetlands, river banks, cliffs) or in the isolated examples of Afro-montane forest.

Quadrat size

In the species-area curve prepared in the Grassy Dwarf Shrublands, a $100m^2$ quadrat provided 70% of the information contained in a 1600 m^2 plot. In the Succulent Dwarf Shrubland, a $100m^2$ (10m x 10m) quadrat provided 66% of the information contained in $300m^2$. In the Succulent Thicket, sample area was varied to accommodate the structural differences between bushclumps and Grasslands or Dwarf Shrublands. The sample boundary was laid out around a bushclump, it was not regular and the total area was variable. Details of the grass or herb layer between the clumps were noted as a separate list of species, although for the purposes of syntaxonomical description all the floristic information about a site was included. In the Shrubland, a clump was included in a $100m^2$ quadrat, where the clumps represent 10% or more of the cover on a landscape. The presence of the woody species in these quadrats is therefore higher than in the landscape.

Data collection

The field data sheet (EC2) of the Botanical Research Institute was completed at each site (Anon 1985). I estimated percentage projected canopy cover subjectively and allocated cover abundance values according to the scale of Barkman *et al.* (1964) in which the scale unit 2 is sub-divided into 2m, 2a and 2b. The number of the LSU, as well as a brief description of its classification in the region, was recorded. Where detailed spectral reflectance information was available, this was provided.

Voucher specimens of all the plant species encountered were submitted to the National Herbarium, Pretoria (PRE), for identification. Duplicates were retained and when a positive

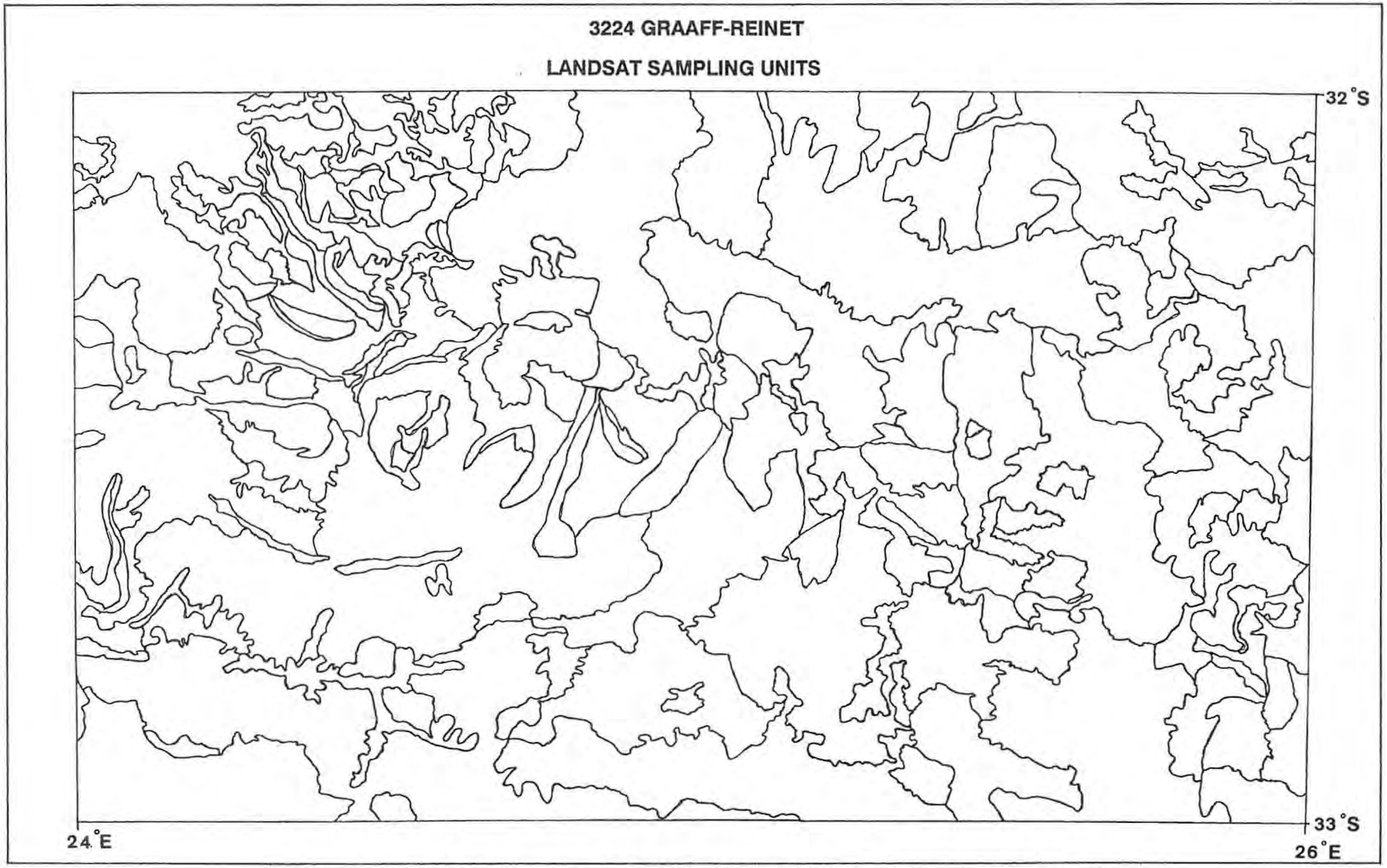


Figure 6. Landsat Sampling Units (LSU's) identified on 3224 Graaff-Reinet from three- band colour composites.

identification for a species was received, one of the duplicate specimens was mounted and curated in a local herbarium on the Karoo Nature Reserve (KNR), Graaff-Reinet and the other donated to the Albany Museum Herbarium (GRA), Grahamstown. Specimens donated by other collectors contributed to this collection (Palmer 1988b).

Environmental variables were recorded in each quadrat (Table 1) and summarized for each community after completion of the phytosociological classification (Table 2). In selected quadrats, soil samples were collected for further analysis. Details of the methods and findings of this aspect of the study area presented by Palmer (1988c). Photographic and cartographic information relating to the location and structure of the sampling site were appended.

The published rainfall isohyets for the region (Venter *et al.* 1986) proved inadequate for assessing the relationship between a precipitation gradient and the vegetation. Mean annual rainfall, compiled from stations with records of 20 years and more (Erasmus 1987), was used to classify the 184 stations into one of seven classes: 200-250mm, 251-300mm, 301-350mm, 351-400mm, 401-450mm, 451-500mm and >500mm. Isohyets (50mm) were hand drawn to enclose the stations within the lines, with contours altered to coincide with major topographical features (Figure 7). A long-term data set for the eastern Cape was extracted from the rainfall records for Grahamstown, and this was combined with the results of Vogel (1988) to show the the oscillation of the annual rainfall about the mean (Figure 8). These simultaneously presented qualitative and quantitative data must be viewed with caution.

Data analysis and synthesis

Methodologies to analyze total floristic data and prepare hierarchical community classification have been dependant on the development of the computer. The early tabulation techniques (Shimwell 1971) necessitate the manual re-arrangement of the columns (quadrats) and rows (species) until an acceptable final phytosociological table (Werger 1974) has been achieved. Early efforts at computerized sorting were those of Ceska & Roemer (1971) using reciprocal averaging sub-routines (Hill 1971). Having used this procedure to develop a phytosociological classification for the plant communities of the Andries Vosloo Kudu Reserve (AVKR) (Palmer 1981), I was dissatisfied with the result. Making use of a simple manual tabulation procedure using a dedicated word processer (Palmer & Lubke 1982), I re-arranged the tables after applying two-way indicator species analysis (Twinspan) (Hill 1979a) to the complete data set. I used the default parameters offered by Twinspan, with the exception of requesting all species to appear in the final tabulation. The final product approaches the classical methods of the Zürich-Montpellier school.

Table 1. Details of the environmental variables recorded at quadrats during the survey.

VARIABLE	METHOD
NUMBER	Sequential ARP1 - ARP290
LOCATION	Co-ordinates determined from Topo Maps
ALTITUDE	Estimated from Topo Series Maps
PHOTOGRAPHIC RECORD	Details of monochrome and Ektachrome recorded
VELD TYPE	Determined from 1:250000 enlargements of Acocks (1953)
FORMATION	According to Edwards (1983)
DOMINANTS	Subjective assessment of dominant species
GEOLOGY	After Johnson & Keyser (1976) and Visser (1986)
GEOMORPHOLOGY	Landform descriptions from Gabriel & Talbot (1984)
EROSION STATUS	1 (low) - 5 (high)
ASPECT	Measured using a compass. Converted to N,NE,E,SE,S etc.
SLOPE	Abney level (^{o})
EXPOSURE	Usually open, rarely protected by overhangs etc.
BIOTIC INFLUENCES	Special note of any biotic influences
SOIL TYPE	According to MacVicar *et al.* (1974)
SOIL DEPTH	Measured when auger hole drilled. Otherwise estimated.
WATERTABLE	Estimated
LANDSAT SAMPLING NUMBER	Read from classified working map
SOIL ANALYSIS	(carried out for selected quadrats)
Texture	Pipette analysis
pH	In KCl and H_2O
Extractable cations	1 N NH_4 acetate leachate
S-value	sum of extractable cations
Oxidizable carbon	% weight after burning
Moisture	% weight after dessication
Available phosphorus	Bray No. 2 acid extraction

Table 2. A summary of the major environmental variables associated with each community.

Legend: Formation: g = Grassland, s = Shrubland, gds = Grassy Dwarf Shrubland, sds = Succulent Dwarf Shrubland, ds = Dwarf Shrubland, st = Succulent Thicket, rt = Riparian Thicket.
Geology: s = sandstone, m = mudstone, d = dolerite, a = alluvium, l = lidianite
Landform: co = concave slopes, cs = convex slopes, p = pediment, pl = plateau, rr = rocky ridge, b = bottomland, co/s = convex and concave slopes.
Erosion Index: 1 = O-horizon intact, 2 = O-horizon absent, 3 = initial erosion of A-horizon, 4 = moderate erosion of A-horizon, and pedestal formation, 5 = excessive erosion of A-horizon with plinthite exposed.
Aspect: 0 = flat with no definite aspect, v = variable, w = mainly west, e = mainly east, n = mainly north, s = mainly south.
Soil Type: m = Mispah, mrc = Mispah rock complex, sli = sandy lithosol, mnd = Mispah/Nyoka/Dudfield association, d = duplex.

Community No.		IA1	IA2	IB1	IIA1	IIA2	IIA3	IIA4	IIA5	IIIA1	IIIA2	IIIB1	IIIC1	IIID1	IVA1	IVA2	IVA3	VA1
Formation		g	g	g	s	s	s	s	gds	gds	gds	ds	ds	sds	st	st	st	rt
Altitude(m)	min	700	1350	1350	727	1270	1330	780	420	970	1000	630	790	690	540	400	490	606
	max	1550	1640	1700	1330	1660	1450	1480	1620	1090	1320	1480	1490	790	980	1060	790	820
Veld Type		42	60	60	37	60	60/37	37	37	37	37	36/38	37/38	38	25	25/37	25	38
Geology		s,d	s,m,d	s,d	s,d	s,d	s,d	s,d,l	s,d	s,d	s,d	s,m,a	s,d,a	s,d,m	s,d	s,d	s,d,m	a,s,d
Landform		co/s	cs	cs	co/s	co/s	cs	co/s	co/s	cs	rr	p	cs	p	co/s	co/s	p	b
			pl	pl			pl	pl	p	p	cs		p					
Erosion Index		1	1	1-4	1-5	1-3	1-2	1-3	1-3	1-2	1-4	1-3	1-5	2-5	1-2	1-3	2-4	1-3
Aspect		v	0,w	v	s,sw	e,w	s,e,w	n-ne	v	n,s,0	n,nw	0	0,ne	0,n	v	n,s	n	0
Slope (^{o})		0-2	0-13	0-4	0-18	4-22	5-22	1-24	0-20	4-13	0-8	0-5	0-5	0-18	0-15	0-15	2-13	0
Soil Type		mrc	mrc	mrc	mrc	sli	mnd	mrc	mrc	sli	sli	sw	sli	mrc	mrc	sli	sli	d
Canopy Cover(%)		75	85	45	55	45	60	40	20	15	40	30	25	10	55	15	65	25
Rockiness (%)		0	0-80	0-20	0-25	0-45	5-30	0-50	10-60	0-65	15-40	0-20	0-15	0-40	0-80	0-50	10-35	0
No. of relevés		3	3	12	11	4	5	14	16	15	13	40	14	11	10	13	5	5

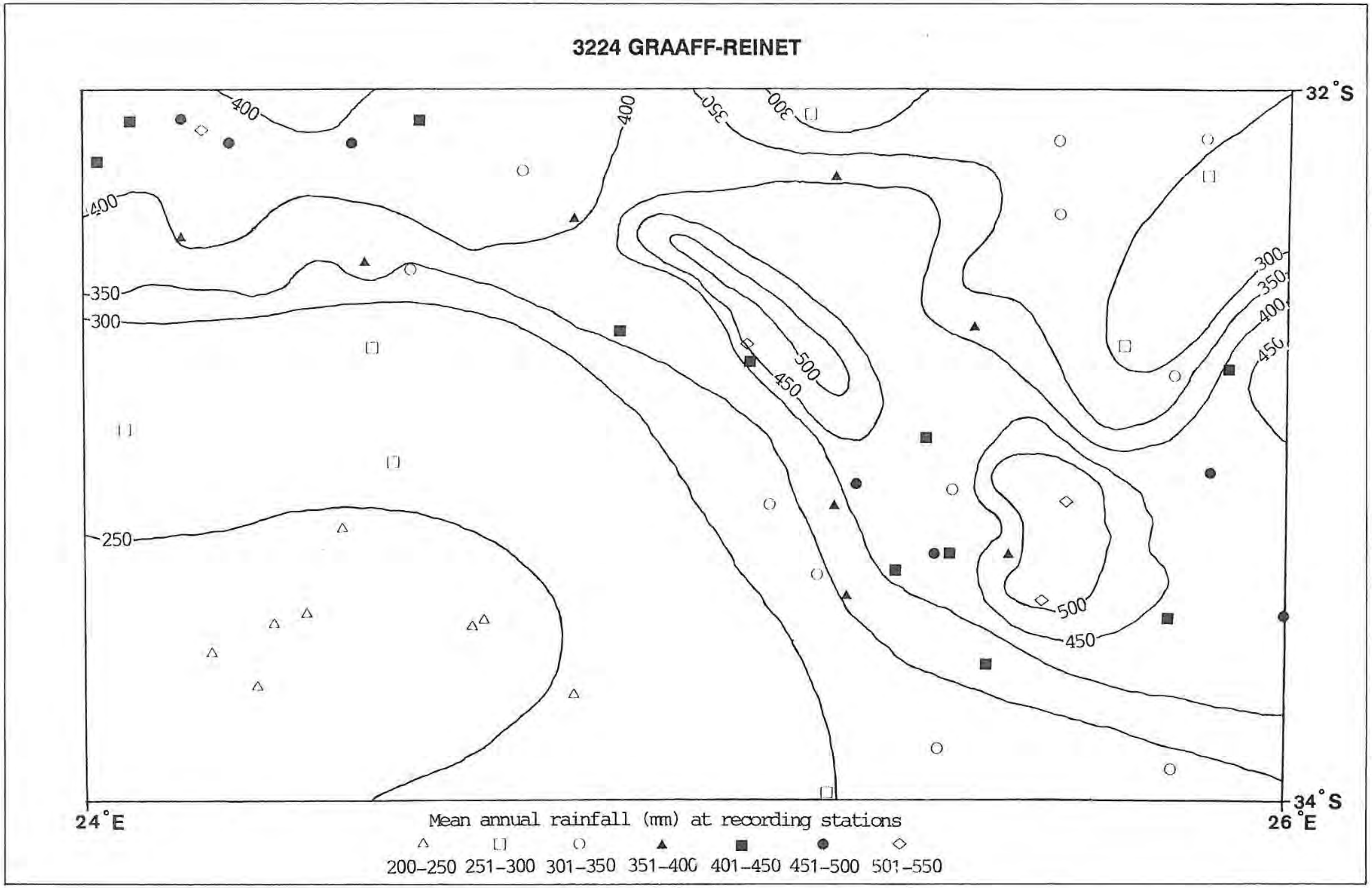
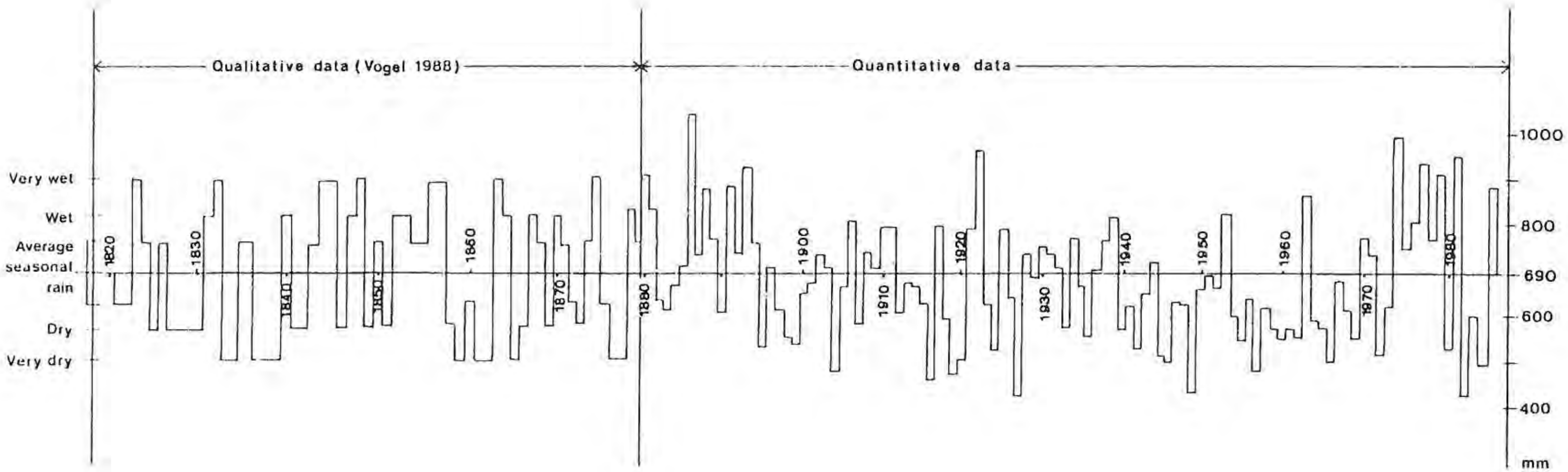


Figure 7. Rainfall isohyets (mm) for 3224 Graaff-Reinet.



RAINFALL OF THE EASTERN CAPE

Figure 8. Long-term rainfall data for the eastern Cape (Vogel, 1988) and Grahamstown, showing variation about the mean for qualitative and quantitative data.

The Anglo-American school of phytosociology (Whittaker 1975) saw the development of computer programmes which subjected the vegetation data set to a variety of ordination procedures known as "indirect gradient analysis" (Whittaker 1967). These procedures have recently been evaluated (Wartenberg *et al.* 1987, Minchin 1987), and Minchin (1987) recommends that local non-metric multidimensional scaling (LNMDS) is a robust technique for indirect gradient analysis which deserves more widespread use. Ordination of the complete data set using Decorana (detrended correspondence analysis) (Hill 1979b) was carried out and ordination diagrams of samples (Figure 9) and species (Figure 10) are presented to aid in the presentation of the syntaxa. The ordination diagrams were plotted using Calcomp plotting routines. The full names for the eighty frequent and differential species in Figure 10 appear in the Appendix. The location of the species in Figure 10 correspond with the symbols for the syntaxa in Figure 9. This product of Decorana provides a visual representation of the species groups and related samples. Criticism has been levelled at Decorana (Swan 1970, Austin & Noy-Meir 1972, Minchin 1987, Wartenberg *et al* 1987), particularly its distortion of inter-stand and inter-species differences (Dargie 1986). I believe its assists in formulating hypotheses and in presenting syntaxonomic concepts, and should continue to be used while taking cognisance of these constraints.

I extracted synoptic or summary tables (Tables 3-9) from the two-way phytosociological tables. These tables "summarize species fidelity to communities within an order and the diagnostic value of species of that order" (Cowling 1983). The presence of each species within each community is rated on a five-point scale and the range of its cover-abundance value is noted: 1 = 1-20% frequency; 2 = 21-40% frequency; 3 = 41-60% frequency; 4 = 61-80% frequency; 5 = >80% frequency. A synoptic table is considered as sufficient original diagnosis if it contains species with a constancy of above 20% (Barkman *et al.* 1986). I regard those species in Tables 3-9 with constancy > 20% as differential species, but have included many species with constancies of <20% and regard these as accompanying species.

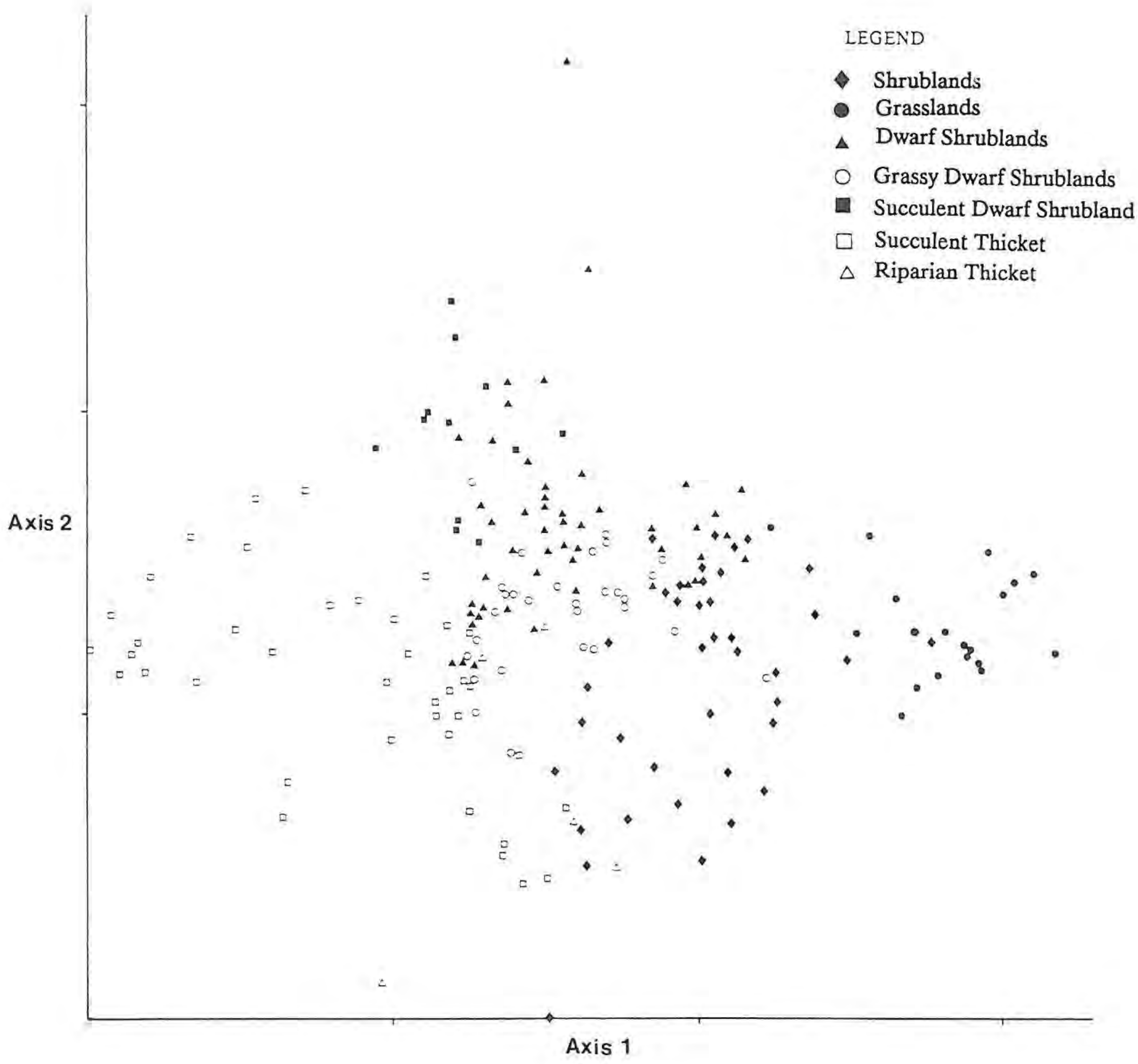


Figure 9. Ordination of samples using Decorana.

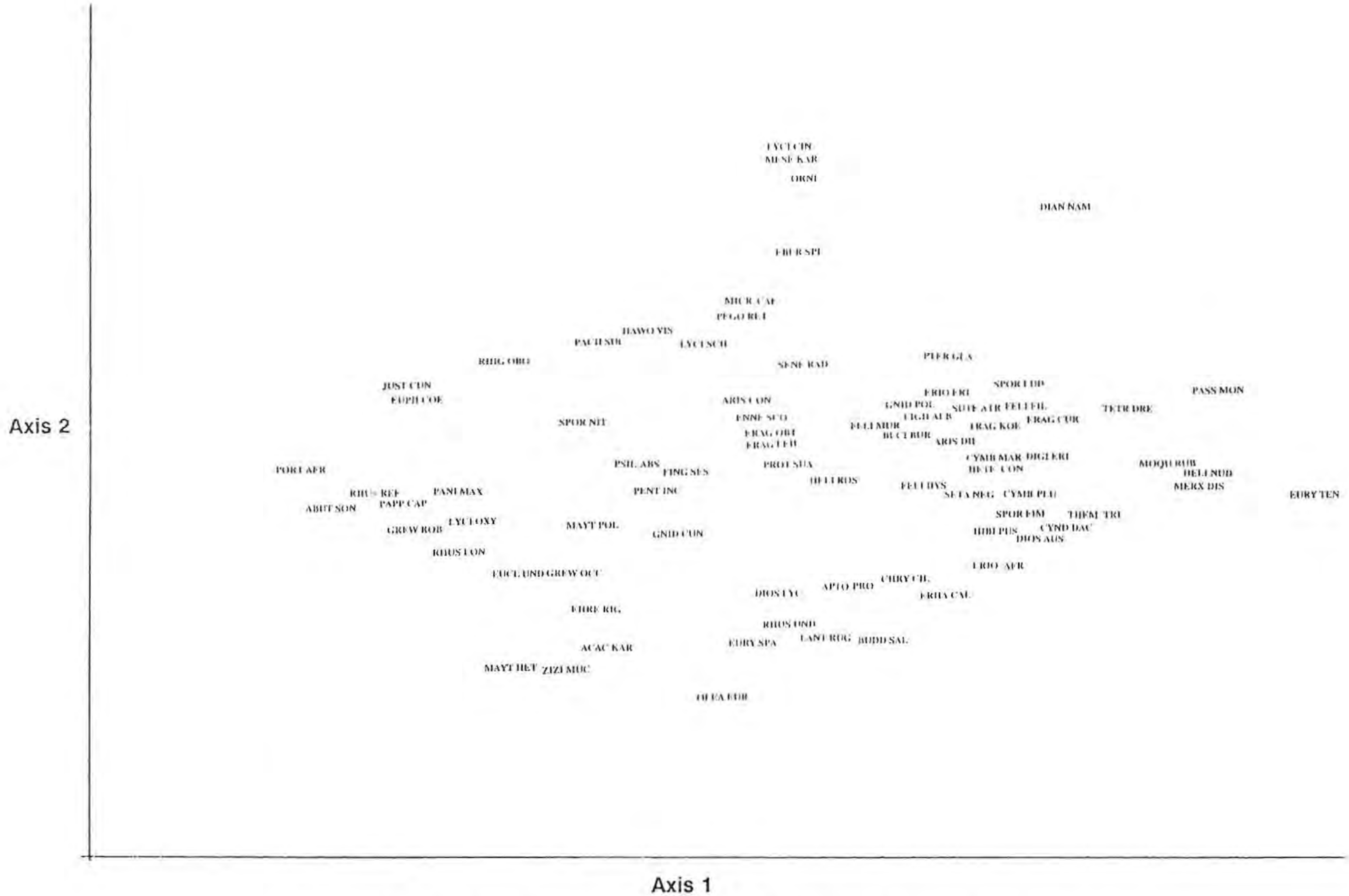


Figure 10. Ordination of species using Decorana. Only selected species have been plotted. See Appendix 1 for species code list.

3.0 THE SYNTAXA

Syntaxonomic ranking

The regional vegetation can be divided into five classes on the basis of broad structural and floristic attributes. These are Karoo Shrublands (*sensu lato* grassy shrubland (White 1983)); Karoo Dwarf Shrublands (*sensu lato* semi-desert vegetation (White 1983)); Sub-Tropical Transitional Thicket (*sensu stricto* Cowling (1983)); Grasslands and Riparian Thicket.

There is a lack of consensus about how to describe the vegetation of the geographical region known as the Karoo. The categories of White (1983) are satisfactory at the level of class. I would like to modify the descriptions of Martin & Noel (1960) and Werger (1980) and suggest the term Dwarf Shrubland to describe the vegetation of the Nama-Karoo biome. This is a change from the "short sparse shrubland" of Edwards (1983), and the "dwarf open shrubland" of Cowling (1986), and allows the use of the adjectives such as "grassy", "succulent" and "degraded" to describe particular states of the Dwarf Shrubland.

The Twinspan tabulation of the total data set parallels the aridity gradient from the mesic grasslands on the left-hand side of the table to the xeric Succulent Dwarf Shrubland on the right- hand side of the table and this trend is summarized in the dendrogram (Figure 11). I retained this general format and during the preparation of the synoptic tables I re-arranged the sequence of differential, frequent and infrequent species extensively. Wherever possible, localities mentioned in the text are followed by the elevation (m) and average annual rainfall (mm) for the nearest station (Erasmus 1987).

My sampling in some cases is not sufficiently intense to extract associations (*sensu* Werger 1974) as the final taxonomic unit. I have termed the ultimate units "communities" without allocating syntaxonomic rank and these may in principle be incorporated into a hierarchical system. In some cases they are equivalent to associations but could mostly be ranked as alliances (Barkman *et al.* 1986).

The main rank in this treatment is the order, which is roughly equivalent to an Acocks (1975) veld type. It is a unit comprising a range of communities which are floristically and structurally related, occurring under broadly similar environmental conditions. I call the highest unit a class which comprises a group of biogeographically related orders.

The code appearing in front of the syntaxa names symbolizes the relationship between the syntaxa.

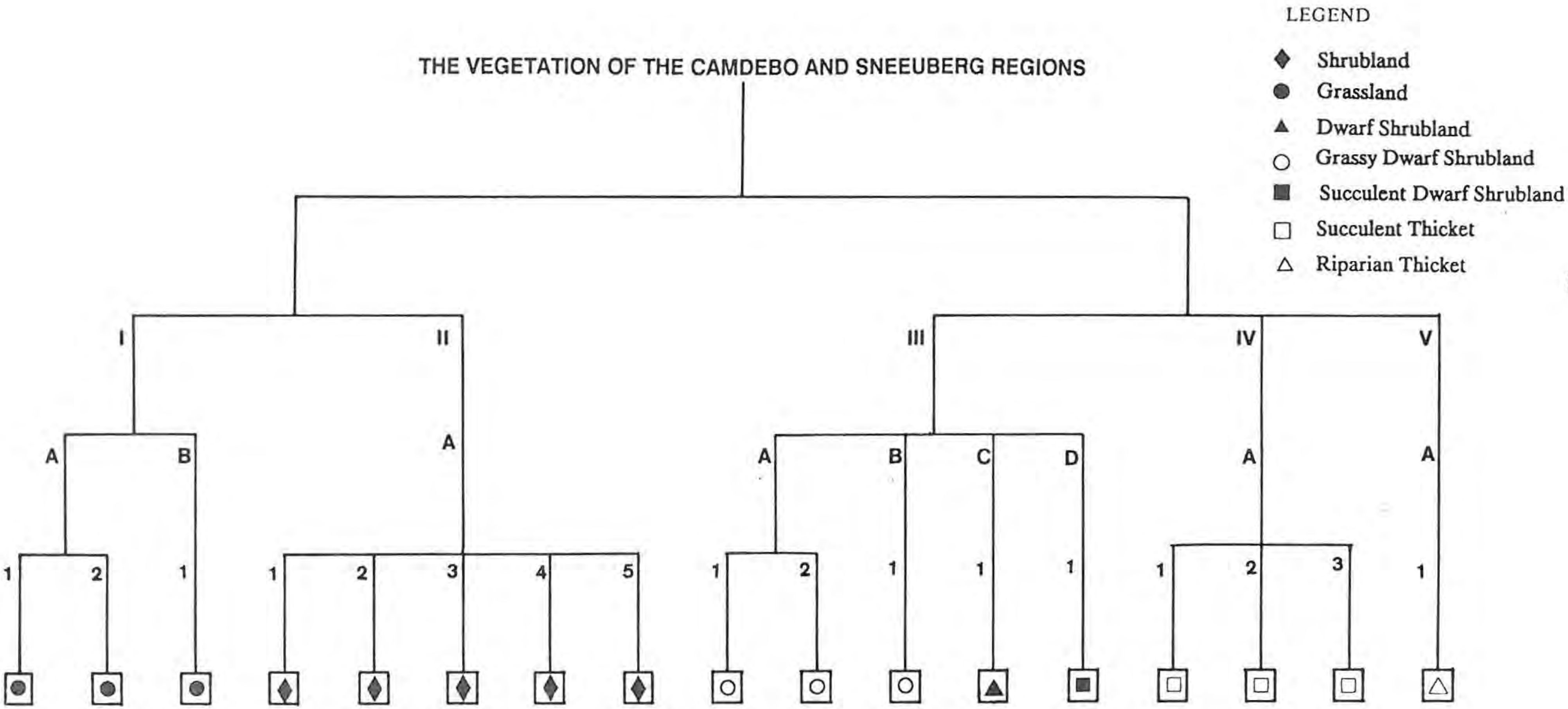


Figure 11. Dendrogram of the hierarchical relationship between communities.

I = class, A = order, 1 = community.

I	Grasslands
IA	Short mesic grasslands of the flat to gently undulating landforms
IA1	*Digitaria eriantha-Themeda triandra* Short Grassland
IA2	*Themeda triandra-Eragrostis chloromelas* Short Grassland
IB	Grasslands of the steeply sloping landforms
IB1	*Merxmuellera disticha-Elytropappas rhinocerotis* Montane Grassland
II	Karoo Shrublands
IIA	Shrublands of the rocky slopes
IIA1	*Euryops spathaceus* Degraded Shrubland
IIA2	*Euclea coriacea-Sutera mollis* Degraded Shrubland
IIA3	*Diospyros austro-africanus* Grassy Shrubland
IIA4	*Chenopodium phillipsianum* Grassy Shrubland
IIA5	*Becium burchellianum* Grassy Shrubland
III	Karoo Dwarf Shrublands
IIIA	Grassy Dwarf Shrublands on the Katberg sandstones of the Cradock region
IIIA1	*Aristida diffusa-Becium burchellianum* Grassy Dwarf Shrubland
IIIA2	*Aptosimum procumbens-Rhus undulata* Broken Dwarf Shrubland
IIIB	The Grassy Dwarf Shrublands of the Camdebo and Aberdeen plains
IIIB1	*Eriocephalus ericoides-Rosenia humulis* Grassy Dwarf Shrubland
IIIC	Dwarf Shrublands (typicum) of the Camdebo
IIIC1	*Euryops anthemoides-Sutera halimifolia* Dwarf Shrubland
IIID	Succulent Dwarf Shrubland
IIID1	*Senecio acutifolius-Haworthia viscosa* Succulent Dwarf Shrubland
IV	Sub-tropical Transitional Thicket
IVA	Succulent Thicket
IVA1	*Abutilon sonneratianum-Portulacaria afra* Succulent Thicket
IVA2	*Maytenus polyacantha-Pappea capensis* Degraded Succulent Thicket
IVA3	*Peliostomum origanoides-Portulacaria afra* Succulent Thicket
V	Riparian Thicket
VA	*Lycium oxycarpum-Maytenus heterophylla* Riparian Thicket

I. GRASSLANDS

The grasslands of the region have been well typified by Acocks (1975) who defined three Veld Types (VT), namely Eastern Province Grassveld (VT 68), Dohne Sourveld (VT 44) and Karroid *Merxmuellera* Mountain Veld (VT 60). Possibly owing to the low sampling intensity, only one

Table 3. Summary table of the differential species of the Grasslands of the Sneeuberg region.

Class	I	I	I
Order number	A	A	B
Community Number	1	2	1
Number of relevés	3	3	12
Differential species of community IA1			
Helichrysum nudifolium	2		
Oxalis bowiei	2		
Indigofera rugosa	1		
Diascia capsularis	1		
Pelargonium abrotanifolium	1		
Protasparagus thunbergii	1		
Cotula sororia	1		
Schismus inermis	1		
Senecio pterophorus	1		
Elionurus argenteus	1		
Differential species of community IA2			
Hyparrhenia hirta		1	
Euryops tenuissimus		1	
Tarconanthus camphoratus		1	
Differential species of community IB1			
Merxmuellera disticha			5
Tragus koeleroides			2
Elytropappus rhinocerotis			2
Pentzia globosa			2
Nenax microphylla			2
Felicia filifolia			2
Diospyros austro-africana		1	2
Rhus erosa		1	2
Heteropogon contortus			2
Aristida diffusa			2
Cymbopogon plurinodis			2
Eriocephalus ericoides			2
Salvia repens			2
Differential species of communities IA1, IA2 and IB1			
Themeda triandra	5	3	3
Eragrostis chloromelas	3	5	5
Passerina montana	1	1	2
Eragrostis curvula	1	1	1
Tetrachne dregei	1	1	2
Melica decumbens	1	1	1
Companion species			
Chrysocoma ciliata			3
Walafrida geniculata		1	
Pentzia incana		1	1

community is defined in each (Table 3).

IA. Short mesic grasslands of the flat to gently undulating landforms

These Grasslands occur on the plateaux and lower pediment sites with high mean annual rainfall (400-650mm). Typical rainfall records (recorded for 20 years and longer) from stations in these grasslands include Somerset East (739 m, 591mm), Oukraal (1158m, 536mm), and Cookhouse (588m, 407mm).

IA1. *Digitaria eriantha-Themeda triandra* Short Grassland

While surveying the vegetation of 1:250 000 Topo Sheet 3224 Graaff-Reinet, I noticed the sharp inter-face between Grassland and Dwarf Shrubland. The abruptness of the interface between Somerset East and Pearston (which had been remarked upon by Barrow (1801)) prompted me to selectively sample this class. High cover-abundance values for *Themeda triandra, Eragrostis chloromelas* and *E. curvula* (Figure 12) are recorded. Elevation varies from 700-1550 m, with the underlying geology dominated by sandstone. The soils are poorly drained, with high moisture content at the time of the survey. A moderately alkaline pH of 6.3 was recorded, together with a relatively high clay fraction of 12.2%. In comparison with soils from other sites in the study area, mineral levels were low (Mg = 17.7 ppm; Ca = 68 ppm; Na = 3.7 ppm). This is most likely a consequence of leaching due to the higher rainfall. Above-ground termitaria are a reliable feature of this community.

Differential and companion species include *Helichrysum nudifolium, Pelargonium abrotanifolium* and *Lycium schizocalyx*. These species correspond well with those listed by Acocks (1975) as being diagnostic of the Eastern Province Grassveld (EPG).

Synonymy: *sensu stricto* Eastern Province Grassveld (Acocks 1975).

IA2. *Themeda triandra-Eragrostis chloromelas* Short Grassland

This community occurs at high elevation at Sterkwater (1623 m), near the homestead at Compassberg (1635 m) and on the Ouberg (1640 m). Dominated by *Themeda triandra* and *Eragrostis chloromelas*, these Grasslands contain a species-rich mesic flora (Figure 13). Infrequent species, which would probably appear as differential species in larger sample set include *Tetrachne dregei, Selago albida, Argyrolobium collinum, Schizoglossum aschersonianum, Bromus leptoclados, Elionurus argenteus, Hyparrhenia hirta, Helictotrichon turgidulum, Schismus inermis, Senecio pterophorus, Euryops tenuissimus, Tarconanthus camphoratus, Helichrysum nudifolium* and *Protasparagus thunbergii*.

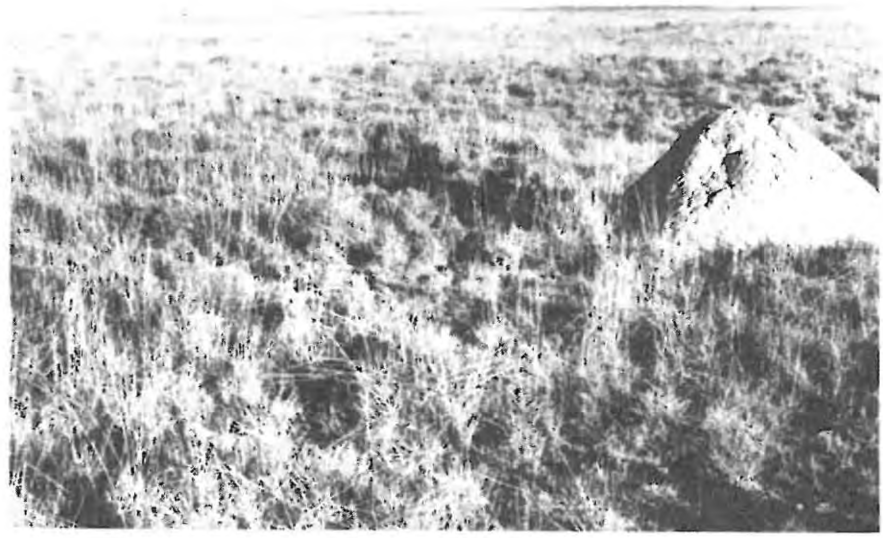


Figure 12. *Digitaria eriantha-Themeda triandra* Short Grassland near Somerset East. Dominant species are *Eragrosrtis curvula, E. chloromelas, Digitaria eriantha* and *Themeda triandra*

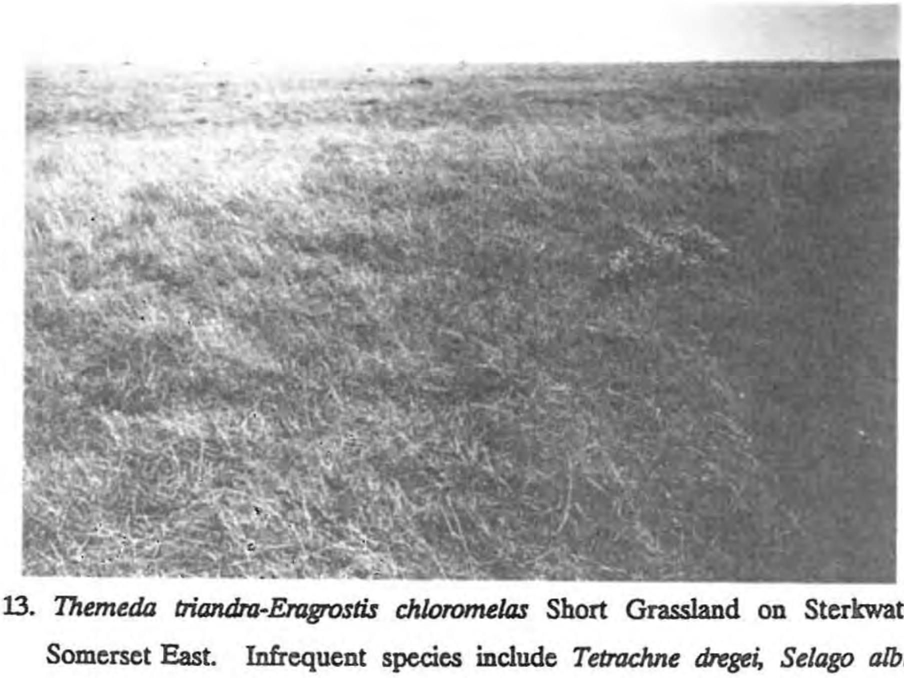


Figure 13. *Themeda triandra-Eragrostis chloromelas* Short Grassland on Sterkwater near Somerset East. Infrequent species include *Tetrachne dregei, Selago albida* and *Helichrysum nudifolium*.

Soil analysis of a site on the farm Sterkwater, revealed low concentrations of minerals (Mg, Ca, K, Na and P), as well as a low pH (5.4). This suggests leaching of the upper soil and a low nutrient status for these grasslands.

Synonymy: *sensu stricto* Dohne Sourveld (Acocks 1975).

IB. Grasslands of the steeply sloping landforms

IB1. *Merxmuellera disticha-Elytropappus rhinocerotis* Montane Grasslands

Merxmuellera disticha is the only differential species with high cover-abundance values. Other differential species include *Felicia filifolia, Cymbopogon plurinodis, Pentzia globosa, Elytropappus rhinocerotis* and *Nenax microphylla*. Species also found in mesic grasslands are *Themeda triandra, Tetrachne dregei, Passerina montana* and *Melica decumbens.*

These dry Grasslands of the steeply sloping landforms follow the aridity gradient from left to right across the phytosociological table. The arid conditions at Nieu-Bethesda (1350m, 383mm) contrast with those experienced 30 km away at Compassberg. Rainfall is marginally higher than Graaff-Reinet, with the same unimodal peak in late summer. This contrasts with the bimodal rainfall of St. Olives, Somerset East and Katbosch.

The geology ranges from sandstone to a mixture of blue and grey mudstone. Dolerite rocks are present in many of the relevés, which are predominantly flat to north-facing, suggesting greater aridity. The soils are a sandy-loam in a Mispah-Rock complex with moderately high Ca levels (112 ppm). Soil pH is moderately low (6.2) when compared with other soils in the study area.

In accordance with the syntaxon typified by Acocks (1975), the following species are of infrequent occurrence: *Karroochloa purpurea, Polygala leptophylla, Pelargonium reniforme, P. myrrhifolium* var. *myrrhifolium* and *Dianthus namaensis*.

Synonymy: *sensu stricto* Karroid *Merxmuellera* Mountain Veld (Acocks 1975)

II. KAROO SHRUBLANDS

IIA. Shrublands of the rocky slopes

The shrublands of the Karoo-Namib region have been well documented by Werger (1980). Generally they occur on steep, rocky slopes and the soils are mainly shallow, neutral to slightly acid lithosols. The Shrublands have an open structure, with shrub densities seldom exceeding 10% of landscape cover. The cover between the shrubs may consist of grasses, dwarf shrubs or a combination of both (Table 4). These differences may be a consequence of the immediate management history of the area.

Synonymy: *sensu stricto* Rhoetea erosae (Werger 1980), *sensu lato* False Karroid Broken Veld (Acocks 1975)

IIA1 *Euryops spathaceus* Degraded Shrubland

In areas of high rainfall (>450 mm per annum) the order is characterized by an increase in the incidence and cover of the genus *Rhus*. Differential species include *Rhus longispina, R. undulata, Euryops spathaceus, Grewia robusta* and *Ehretia rigida*. Companion species are dominated by *Pentzia incana*, with few grasses represented. Clumps may cover up to 50% of the relevé.

Altitude varies from 727-1330 m, with the geology predominantly sandstone and dolerite. Relevés have a southerly aspect, with rockiness varying from 0-80%.

IIA2. *Euclea coriacea-Sutera mollis* Degraded Shrubland

Situated at moderately high elevations (1270-1660 m), this is a degraded form of the Shrublands in a mesic environment. The terrain is gently to steeply sloping, with sandstones and scattered dolerite boulders (Figure 14). Excessive erosion is evident between the dwarf shrubs. Shrubs are not a major feature of this community and dwarf shrubs may account for as much as 60% of cover. The differential species include *Euclea coriacea, Sutera mollis, Elytropappus rhinocerotis* and *Mestoklema albanicum*. Companion species include *Chrysocoma ciliata, Aristida diffusa, Pentzia incana* and *Merxmuellera disticha*. These relevés represent a condition in which the grass component has been replaced by dwarf shrubs. Differential species include the woody shrubs *Rhus undulata, Buddleja saligna* and *Rhus erosa*. Infrequent species include *Eustachys paspaloides, Aloe broomii* var. *tarkaensis* and *Ehrharta calycina*.

IIA3. *Diospyros austro-africanus* Grassy Shrubland

Relevés are located on the cool east- or south-facing slopes and elevation of the relevés varies from 1330-1450m. The parent geology ranges from dolerite to dolerite boulders on sandstone, with the soils being classified as a Mispah-Rock complex. The total cover values for these relevés is high (60-80%), with woody shrubs cover accounting for 15-45% of total vegetative cover (Figure 15). Differential species include *Diospyros austro-africanus, Olea europaea* subsp.

Figure 14. *Euclea coriacea-Sutera mollis* Degraded Shrubland at the Valley of Desolation, Graaff-Reinet. Differential woody species include *Rhus undulata, Buddelja saligna* and *Rhus erosa.*

Figure 15. *Diospyros austro-africanus* Grassy Shrubland, with *Rhus erosa* in the foreground.

Table 4. A summary table of the differential and companion species of the Shrublands of the Camdebo and Sneeuberg regions of the Nama-Karoo biome.

Class			II		
Order			A		
Community	1	2	3	4	5
Number of relevés	11	4	5	14	16
Differential species of community IIA1					
Grewia robusta	3		1		
Rhus longispina	3				
Cynodon incompletus	3				
Ehretia rigida	1		1		
Differential species of community IIA2					
Euclea coriacea		3			
Sutera mollis		3		1	
Mestoklema albanicum		1	2		
Aloe broomii		1	1		
Differential species of of community IIA3					
Diospyros austro-africana			5	2	1
Elytropappus rhinocerotis			3	1	1
Rhus erosa		1	2	1	2
Crassula muscosa		1	2		1
Sutera halimifolia			1		
Selago corymbosa			2		
Olea europaea			1	1	
Differential species of of community IIA4					
Grewia occidentalis				2	
Chenopodium phillipsianum				2	
Sporobolus fimbriatus				2	
Aristida congesta				2	1
Indigofera heterophylla				2	1
Teucrium africanum				3	
Melica decumbens				2	
Solanum coccineum				3	
Helichrysum cymosum				2	
Eragrostis chloromelas				3	1
Lantana rugosa				2	
Solanum rigidum				1	
Differential species of of community IIA5					
Eragrostis curvula				1	2
Nenax microphylla		1		1	1
Becium burchellianum					3
Melolobium candicans				1	
Tragus racemosus					2
Helichrysum dregeanum					1
Eriocephalus umbellatus					1
Differential species of of communities IIA4 & 5					
Heteropogon contortus				4	5
Digitaria eriantha			1	4	2
Indigofera sessilifolia				3	1
Eriocephalus africanus				4	1
Enneapogon scoparius				3	2
Cymbopogon plurinodis			1	3	1
Differential species of of communities IIA1-5					
Rhus undulata	5	1	3	3	1
Acacia karroo	4			3	2
Maytenus polyacantha	1		2	1	1
Ehrharta calycina	2	1	2	1	1
Euclea undulata	1		3		1
Euryops spathaceus	3		5		1
Buddleja saligna	1	3	1	1	1
Companion species					
Pentzia incana	5	1	3	4	3
Chrysocoma ciliata	1	5	5	4	3
Themeda triandra	1	1	2	5	4
Walafrida geniculata	1		3		2
Eragrostis lehmanniana	1		3	1	3

africana, Blepharis villosa, Euclea undulata, Euryops spathaceus, Rhus undulata and *R. erosa*. Companion species include *Pentzia incana, Chrysocoma ciliata* and *Themeda triandra* . The general condition of relevés vary from "over-utilized by domestic stock" to "protected from utilization due to inaccessibility".

IIA4. *Chenopodium phillipsianum* Grassy Shrubland

The elevation of the relevés in this community varies from 780-1480 m, with many being lower than those of IIA3. The landforms are convex and well drained, with a northerly aspect. Total vegetative cover is lower than in IIA3, varying from 30-80 %, with woody shrubs accounting for 10-50% of total vegetative cover. Dolerite is present in all the relevés, with sandstone and lidianite being found in some cases. The grassiness was accounted for by *Digitaria eriantha, Themeda triandra, Eragrostis chloromelas, Hyparrhenia hirta, Eustachys paspaloides, Cymbopogon plurinodis,* and *Heteropogon contortus*. Differential species include *Teucrium africanum, Eriocephalus africanus, Lantana rugosa, Helichrysum cymosum, Solanum coccineum, Walafrida saxatilis* and *Chenopodium phillipsianum*. Woody shrubs which are differential species include *Grewia occidentilis* and *Rhus undulata*.

IIA5. *Becium burchellianum* Grassy Shrubland

Differential species are the dwarf shrubs *Eriocephalus umbellatus, Tragus racemosus, Helichrysum dregeanum* and *Becium burchellianum*. Woody shrubs are rare, but include *Maytenus polyacantha, Rhus erosa* and *R. undulata*. Grasses are abundant, with *Aristida diffusa, Eragrostis lehmanniana, E. obtusa, Themeda triandra, Heteropogon contortus* and *Tragus koeleroides* appearing in one relevé.

In the vicinity of the Mountain Zebra National Park (MZNP), Acocks regards VT 42 as a product of anthropogenic influence. It is one of the smallest Veld Types, measuring some 2250 km^2 (Scheepers 1983) in extent. Van der Walt (1980) describes a *Becium burchellianum* community on the plateaux in the MZNP, and suggests this is a product of localized over-grazing. The data in the survey by Van der Walt (1980) suggests that this community has high cover values for species adapted to shallow stoney soils (Figure 16). *B. burchellianum* is a regional endemic (Palmer 1988f) and is associated with prominent sandstone outcrops. During the assessment of the use of Landsat imagery to map vegetation in the Karoo, I recognized the boundaries of a sampling unit in the region which corresponds accurately with the boundaries of VT 42 and I suggest that these boundaries correspond with areas of geological discontinuity.

Synonymy: *sensu stricto* Karroid *Merxmuellera* Mountain Veld replaced by Karoo (Acocks 1975).

III. KAROO DWARF SHRUBLANDS

The Dwarf Shrublands occur on the gently sloping, arid pediments between the mountain ranges. Structureless to weakly structured soils are a feature of these pedologically young landscapes. The soils have generally developed *in situ* from colluvium, with lime present in the entire landscape, and the Mispah and Glenrosa forms predominate (Ellis & Lambrechts 1986). The low, irregular precipitation patterns, and the increasing aridity from east to west contribute towards the mosaic of communities near Cradock (880m, 334mm), Graaff-Reinet (727m, 353mm), Aberdeen (732, 284mm) and Pearston (710m, 328mm). The communities I describe extend from the Grassy Dwarf Shrublands in the east to the Succulent Dwarf Shrublands in the west (Tables 5 & 6). On the boundaries of the Dwarf Shrublands, at contact with Succulent Thicket or Grasslands, transitional communities, colloquially known as "apron-veld", occur. I refer to this as the vegetation of the foot-slopes.

IIIA. Grassy Dwarf Shrublands on the Katberg sandstones of the Cradock region

The principal sampling site in the eastern section of the study area is situated in the Commando Drift Nature Reserve (CDNR), which surrounds the Commando Drift reservoir at the confluence of the Tarka, Elands, Vlekpoort and Paling rivers (25° 59 E, 32° 02 S). I divided the plant communities of this nature reserve into four units, each containing grasses as differential species (Palmer 1979). These data were included in this study. The relevés have been classified as the grassy form of the Karoo Dwarf Shrublands (Table 5), with differential species being *Aristida diffusa, Eragrostis obtusa, Enneapogon scoparius, Heteropogon contortus, Thesium hystrix, Helichrysum rosum, Chrysocoma ciliata, Indigofera sessilifolia* and *Themeda triandra*. Companion species include *Digitaria eriantha, Cymbopogon plurinodis* and *Eragrostis curvula.*

The communities occur on the fossiliferous beds of the Katberg Sandstone Formation (Johnson & Keyser 1976). At this position the beds are approximately 500 m thick and mudstone constitutes about 30 % of the formation. Horizontal lamination and cross bedding characterize the sandstone, and the mudstone is generally massive. The higher percentage of mudstone has accelerated the formation of alluvium in this area and resulted in the formation of deep, duplex soils (i.e. having a structureless A-horizon and a clayey, structureless B-horizon). These duplex soils are susceptible to exceptionally severe erosion, leading to the formation of the so-called "Vlekpoort erosion area". The sedimentary rocks have been intruded, creating rocky ridges and convex sloping mountains.

Table 5. A summary table of the differential and companion species of the Grassy Dwarf Shrublands of the Katberg sandstones of the Cradock region.

Class	III	
Order	A	
Community	1	2
Number of relevés	15	13
Differential species of community IIIA1		
Melolobium candicans	1	
Tragus koeleroides	2	2
Blepharis capensis	1	1
Indigofera alternans	2	1
Ehretia rigida	1	
Nenax microphylla	2	
Limeum aethiopicum	2	
Becium burchellianum	2	
Tragus racemosus	3	2
Helichrysum zeyheri	2	1
Felicia muricata	2	
Nemesia floribunda	2	
Microchloa caffra	1	
Moraea polystachya	2	
Paspalum sp.	1	
Differential species of community IIIA2		
Rhus undulata		2
Lycium oxycarpum	1	1
Setaria sphacelata		1
Sutera pinnatifida		1
Blepharis villosa		1
Aptosimum procumbens		2
Crassula obovata		2
Differential species of community IIIA1 and IIIA2		
Enneapogon scoparius	5	5
Aristida diffusa	4	3
Eragrostis obtusa	2	3
Helichrysum rosum	1	2
Chrysocoma ciliata	1	4
Heteropogon contortus	1	1
Thesium hystrix	2	2
Indigofera sessilifolia	1	1
Themeda triandra	1	1
Companion species		
Pentzia incana	5	5
Eragrostis lehmanniana	5	3
Aristida congesta	5	1
Protasparagus plumossus	1	1
Eriocephalus umbellatus	1	1
Lightfootia albens	1	1

Figure 16. *Becium burchellianum* Grassy Shrubland near the Mountain Zebra National Park.

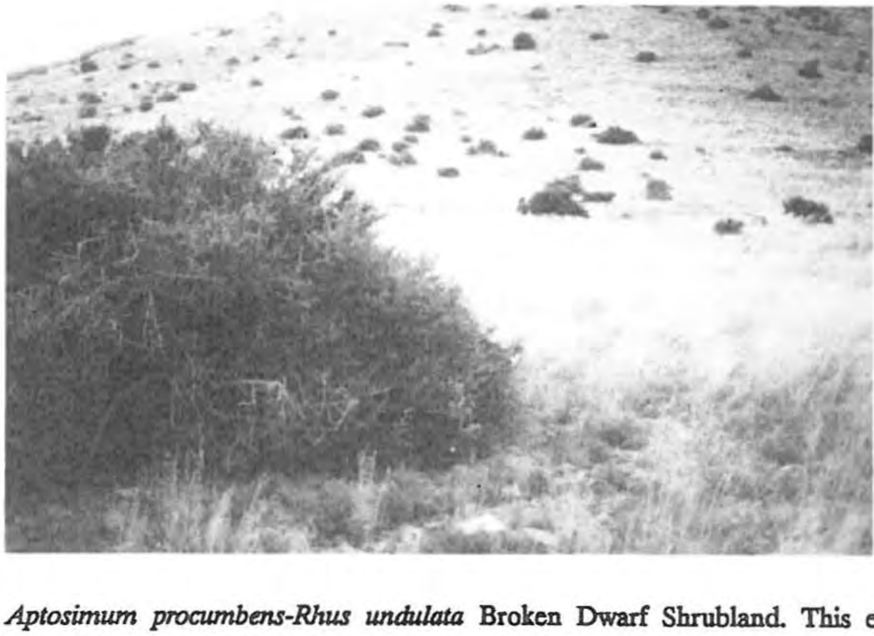


Figure 17. *Aptosimum procumbens-Rhus undulata* Broken Dwarf Shrubland. This example of the Grassy Dwarf Shrubland contains grasses *Setaria spacelata*, *Eragrostis lehmanniana* and *Aristida diffusa* in the foreground.

IIIA1. *Aristida diffusa-Becium burchellianum* Grassy Dwarf Shrublands

The differential species are *Becium burchellianum, Felicia muricata, Melolobium candicans, Blepharis capensis, Moraea polystachya* and *Nemesia floribunda.* Companion species include *Pentzia incana, Eragrostis lehmanniana* and *Aristida congesta*. The landform is a gently sloping to flat sandstone and dolerite ridge. The soils are shallow (30-50 cm), light brown, sandy loams. Percentage canopy cover varies from 15-80%, rockiness from 0-65%, and grassiness varying from 40-75%.

Rare and infrequent species include *Hermannia vestita, Fingerhuthia sesleriiformis, Convolvulus sagittatus* var. *ulosepalus* and *Tetragonia echinata.* Relevés on the CDNR showed evidence of recent disturbance due to grazing by domestic ungulates, with a high incidence of grasses of low palatability to ungulates. Post-disturbance recovery is good, with an increase in the incidence of more palatable grasses. I suggest that the trend towards a more grassy condition will continue.

IIIA2. *Aptosimum procumbens-Rhus undulata* Broken Dwarf Shrublands

The differential species include *Aptosimum procumbens, Setaria sphacelata, Rhus undulata* and *Crassula obovata.* Companion species are *Pentzia incana, Eragrostis lehmanniana* and *Aristida congesta. Rhus undulata, Diospyros lycioides* and *Acacia karroo* account for the brokeness of the landscape (Figure 17), however their percentage contribution to canopy cover is <10%. The terrain in which this community occurs is very rocky, with sandstone and dolerite mixed in various proportions. Aspect is flat to north-facing, with the associated tendency towards greater aridity. Elevation varies from 1020-1330 m. The soils are all shallow, sandy loams. Infrequent species include *Enneapogon desvauxii, Hertia pallens, Dicoma spinosa* and *Pegolettia retrofracta.*

Synonymy: *sensu lato* False Karroid Broken Veld (Acocks 1975).

IIIB. The Grassy Dwarf Shrublands of the Camdebo and Aberdeen plains

The Camdebo and Aberdeen pediments are characterized by two well represented communities (Table 6) which cover a large area of these plains. The relationship between vegetation and environment is difficult to unravel, as a mosaic of communities may exist. The activities of small mammals inhabiting these plains contribute to the mosaic by creating areas of disturbance up to 300 m^2 in area (Palmer 1987).

A synonymous order, the PENTZIETEA INCANAE, occurs in the rocky soils of the western upper Orange river valley (Werger 1980). The intruding species of the PENTZIO-CHRYSOCOMION (Werger 1980) are an important distinguishing feature of the order.

Table 6. A summary table of the differential and companion species of the Grassy Dwarf Shrublands of the Camdebo and Aberdeen plains.

Class	III
Order	B
Community	1
Number of relevés	40
Differential species of community IIIB1	
Lycium schizocalyx	4
Eragrostis obtusa	3
Rosenia humulis	3
Eragrostis lehmanniana	2
Eberlanzia spinosa	2
Blepharis villosa	2
Eriocephalus ericoides	2
Galenia sarcophylla	2
Protasparagus suaveolens	1
Mestoklema tuberosum	1
Aristida diffusa	1
Felicia filifolia	1
Pegolettia retrofracta	1
Thesium hystrix	1
Trichodiadema bulbosum	1
Melicia racemosa	1
Thesium rigidum	1
Helichrysum zeyheri	1
Sutera pinnatifida	1
Tragus racemosus	1
Eragrostis chloromelas	1
Aptosimum procumbens	1
Gazania linearis	1
Sarcocaulon camdeboense	1
Indigofera sessilifolia	1
Enneapogon scoparius	1
Microchloa caffra	1
Companion species	
Pentzia incana	5
Aristida congesta	5
Chrysocoma ciliata	3
Felicia muricata	3
Tragus koeleroides	2
Senecio acutifolius	1
Hibiscus pusillus	1
Eragrostis curvula	1
Digitaria eriantha	1
Merxmuellera disticha	1
Nenax microphylla	1
Helichrysum dregeanum	1
Helichrysum rosum	1
Hermannia cuneifolia	1
Euphorbia ferox	1
Cynodon incompletus	1
Lepidium africanum	1
Atriplex semibaccata	1
Limeum aethiopicum	1
Walafrida geniculata	1

However, the hypothesis that these are intruding species has not been fully tested and the differential species suggested by Werger (1980) do not retain their fidelity to the order. I suggest that the intruding species of the PENTZIO-CHRYSOCOMION be included in the differential species of the order PENTZIETEA INCANAE.

Synonymy: *sensu stricto* Pentzietea incanae (Werger 1980)

IIIB1. *Eriocephalus ericoides-Rosenia humulis* Grassy Dwarf Shrubland.
This community occurs on the flat to gently sloping pediments where the substrate consists of pedologically young soils derived from colluvium on more resistant sandstone and dolerite. Relevés are not located on the deep structureless Quaternary alluvia, but rather on shallow soils (10-50 cm) that have developed *in situ*. Soil pH (H_2O) is weakly to strongly alkaline (6.7-7.6) with high Ca (156 ppm) and Na (4.1-13.2 ppm) levels. The presence of limestone ($CaCO_3$) at ±30 cm below the surface is a common feature. There does not appear to be a predictable relationship between the seriousness of the erosion and the presence or absence of any of the differential species.

The growth forms include microphyllous dwarf shrubs, succulent dwarf shrubs, deciduous shrubs and grass (Figure 18). In a subjective structural analysis of the relevés, annual and weakly perennial grasses account for 20-80% of cover. This grassiness is exemplified by the differential species *Microchloa caffra, Enneapogon scoparius, Schismus inermis, Melica racemosa* and *Eragrostis chloromelas*. Differential species include the dwarf shrubs *Blepharis villosa, Rosenia humulis, Felicia filifolia, Gazania linearis,* and *Helichrysum zeyheri*.

IIIC. Dwarf Shrublands (typicum) of the Camdebo
A feature of the geological ontogeny of the Camdebo is the presence of dolerite sills which encircle the plain, and dykes which traverse it. One of the physiographic effects of the sills is that a raised platform develops and the parent material from which the soil originates is dolerite, giving rise to a shallow Mispah Form with a $CaCO_3$ hardpan. Van Riet & Minnaar (1977) describe this as a Mispah/Nyoka association, with saprolite below the pedocutanic B-horizon. The presence of a calcareous layer in the B-horizon, and the predominantly non-red colour justifies the classification of MacVicar *et al.* (1977). This phenomenon is particularly obvious on the farm Brooklyn where the plateau is not influenced by secondarily transported parent material. The moderately shallow (30cm) soil has a granular texture in the B-horizon. Oxidizing dolerite inclusions are common at a depth of 20cm. The Dwarf Shrubland associated with raised dolerite plateaux is discernable on the Landsat imagery (LSUs' 273, 192, 191).

Figure 18. *Eriocephalus ericoides-Rosenia humulis* Grassy Dwarf Shrubland.

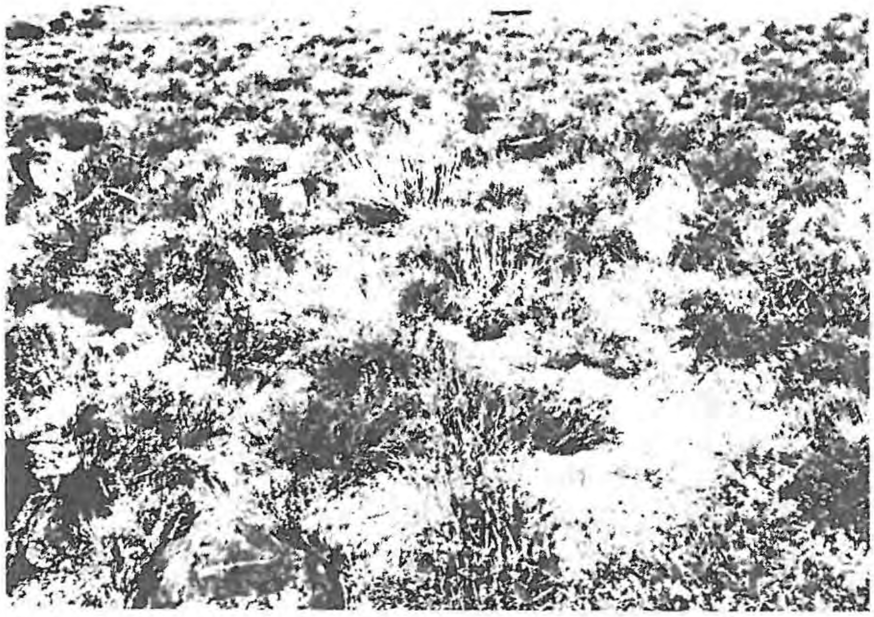


Figure 19. *Senecio acutifolius-Haworthia viscosa* Succulent Dwarf Shrubland in the rocky upper pediment on the Karoo Nature Reserve.

Table 7. A summary table of the differential and companion species of the Dwarf Shrubland *typicum* of the Camdebo and Aberdeen plains.

Class	III
Order	C
Community	1
Number of relevés	14
Differential species of community IIIC1	
Rhigozum obovatum	2
Pachypodium succulentum	2
Haworthia viscosa	1
Sutera halimifolia	2
Polygala hottentota	1
Blepharis capensis	1
Pteronia glauca	1
Euryops anthemoides	2
Indigofera sessilifolia	1
Walafrida geniculata	1
Nenax microphylla	1
Sporobolus ludwigii	1
Eragrostis curvula	2
Gnidia polycephala	1
Merxmuellera disticha	1
Pentzia globosa	1
Lycium schizocalyx	1
Bulbine abyssinica	1
Geigeria ornativa	1
Mesembryanthemum karrooense	1
Ornithogalum sp.	1
Lepidium africanum	1
Blepharis villosa	3
Crassula muscosa	2
Senecio radicans	2
Eberlanzia spinosa	2
Trichodiadema setuliferum	1
Companion species	
Pentzia incana	5
Aristida congesta	5
Eragrostis lehmanniana	4
Eragrostis obtusa	3
Protasparagus suaveolens	3
Chrysocoma ciliata	3
Rosenia humulis	2
Aristida diffusa	2
Aptosimum procumbens	2
Tragus koeleroides	2
Eriocephalus ericoides	1
Felicia filifolia	1
Tragus racemosus	1
Thesium rigidum	1
Pegolettia retrofracta	1
Helichrysum rosum	1
Cadaba aphylla	1

IIIC1. *Euryops anthemoides-Sutera halimifolia* Dwarf Shrubland.

Differential species (Table 7) are dominated by *Blepharis villosa, Eberlanzia spinosa, Crassula muscosa* and *Senecio radicans*. Companion species include *Pentzia incana, Aristida congesta, Eragrostis lehmanniana, E. obtusa* and *Chrysocoma ciliata*. The association between species within the differential species group, for example *Rhigozum obovatum, Pachypodium succulentum* and *Haworthia viscosa*, suggest that further sub-division of this community is necessary.

IIID. Succulent Dwarf Shrubland

Important genera which distinguish this community from others in the class are *Trichodiadema, Ruschia, Anacampseros, Mesembryanthemum, Euphorbia, Eberlanzia, Mestoklema, Crassula* and *Senecio*. Other small-leaved dwarf shrubs (*Pentzia, Eriocephalus, Pteronia*) are present in the landscape, with the weakly perennial grasses appearing after rain.

The presence of numerous Nama-Karoo endemics (Palmer 1988f) suggests that the Succulent Dwarf Shrubland has a phytogeographical affinity with the Nama-Karoo biome. The order characteristically grows on the lower pediments and bottomlands in deep, sandy, sodic soils (Palmer 1988c).

IIID1. *Senecio acutifolius-Haworthia viscosa* Succulent Dwarf Shrubland.

The differential and companion species of this community (Figure 19 & 20) are listed in Table 8. The differential species are Nama-Karoo or regional endemics. The succulent dwarf shrubs which differentiate this community are *Senecio acutifolius, S. radicans, Trichodiadema pygmaeum, Crassula muscosa, Euphorbia ferox, Mestoklema tuberosum* and *Eberlanzia spinosa*. *Pentzia incana, Aristida congesta, Eriocephalus ericoides* and *Lycium schizocalyx* are companion species. Rockiness accounts for up to 40% of cover.

Synonymy: *sensu lato* False Central Lower Karoo (Acocks 1975)

IV. SUB-TROPICAL TRANSITIONAL THICKET

The term "transitional" refers to the uncertain phytochorological affinity of the class. Cowling (1983) reports that many of the succulent species in the class have been classified as Tongaland-Pondoland-Karoo-Namib linking species. Together with Lubke, Tinley & Cowling (1988), I support the suggestion that this class has an affinity with the Tongaland-Pondoland Regional Mosaic (Moll & White 1978).

Figure 20. *Senecio acutifolius-Haworthia viscosa* Succulent Dwarf Shrubland on the lower pediment near Gannalaagte on the Karoo Nature Reserve.

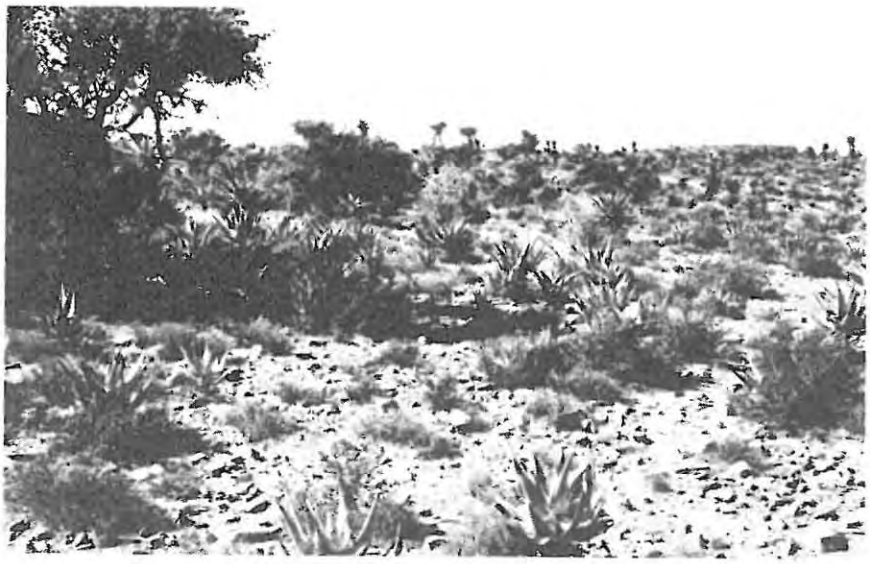


Figure 21. *Maytenus polyacantha-Pappea capensis* Degraded Succulent Thicket.

Table 8. A summary table of the differential and companion species of the Succulent Dwarf Shrubland of the Camdebo.

Class	III
Order	D
Community	1
Number of relevés	11
Differential species of community IIID1	
Senecio longiflorus	4
Senecio acutifolius	5
Haworthia viscosa	3
Trichodiadema pygmaeum	4
Sarcocaulon camdeboense	4
Rhigozum obovatum	4
Eberlanzia spinosa	3
Pachypodium succulentum	4
Bulbine sp.	2
Blepharis villosa	2
Bulbine abyssinica	1
Crassula muscosa	2
Crassula tetragona	1
Senecio radicans	3
Mestoklema tuberosum	3
Protasparagus striatus	3
Euphorbia ferox	3
Anacampseros telephiastrum	1
Ruschia grisea	1
Euphorbia esculenta	1
Galenia sarcophylla	3
Zygophyllum retrofractum	1
Crassula corallina	1
Crassula ericoides	1
Salsola aphylla	1
Psilocaulon absimile	1
Companion species	
Pentzia incana	5
Aristida congesta	5
Lycium schizocalyx	5
Eriocephalus ericoides	2
Rosenia humulis	2
Thesium rigidum	1
Pegolettia retrofracta	2
Eragrostis obtusa	2
Aristida diffusa	2
Felicia filifolia	1
Protaspargus suaveolens	2
Tragus koeleroides	1

In the treatment of the vegetation of the Fish River scrub variation of the Valley Bushveld (Palmer 1981), I describe mesic and xeric variations of the thicket. Cowling (1983) and Everard (1987) incorporate these concepts in Kaffrarian Thicket and Succulent Kaffrarian Thicket. In the Camdebo, I encountered the xeric variation, or Karroid Succulent Thicket (Cowling 1984). I suggest the name Camdebo Succulent Thicket for this order.

IVASucculent Thicket

The communities containing the succulent shrub *Portulacaria afra* and low-growing succulents of the genera *Crassula, Aloe, Cotyledon, Euphorbia, Sarcostemma* and *Lycium* , occur in a belt below the snow line (400-1060 m), yet above the pediments. This belt may be the result of moderate temperatures experienced by these areas during extremely low temperature situations recorded in winter. Low temperatures in the *Portulacaria afra-Euphorbia bothae* sub-association were recorded by Palmer (1981) on the Andries Vosloo Kudu Reserve, but these only persisted for a very short time, whereas above the snowline on the KNR, low temperatures probably persist for much longer periods.

The gradient from the typical Succulent Thicket to the mesic variation occurs along two axes, namely an increase in elevation or movement further eastwards. The minerally rich soils of mudstone origin give way to less basic soils of sandstone origin. There is a decrease in the occurrence of succulence with *P.afra* being replaced by *Rhus incisa* and *Scutia myrtina*. The bushclumps are more clearly defined, and the herbaceous component contains fewer dwarf shrubs. This condition has been described by Martin & Noel (1960) as a bushclump savanna. Low growing *Crassula* spp. are present.

The herbaceous layer varies from a mixed grassy situation during wet periods to a dwarf-shrubland during dry periods. The condition is further exacerbated by the shallow O-horizon (where this is still present) and processes associated with the soil erosion cycle, such as soil capping and the deposition of a shallow silt layer above the A-horizon. The herbaceous communities do not reflect the condition of the order, but rather the recent management history of the site. Different treatments of the vegetation, ranging from intensive non-selective grazing through to very low intensity use, combined and with the option of sporadic fire, indicate that different structural groups may occur adjacently.

Synonymy: *sensu lato* Succulent Mountain Scrub (Spekboomveld), Valley Bushveld, Noorsveld (Acocks 1975); Karroid Succulent Thicket (Cowling 1984).

IVA1 *Abutilon sonneratianum-Portulacaria afra* Succulent Thicket

This community (Table 9) occurs in areas receiving ±300-350mm rain per annum. Occupying both warm and cool slopes, it may assume thicket proportions on slopes covered by dolerite boulders. On the KNR, I describe a *Portulacaria afra-Grewia robusta* Association that reflects the floristics of this community (Palmer 1988a). On the southern aspects, the community is taller (>2,5 m) with a light canopy of *P. afra* developing. Herbaceous cover in the understorey is limited to weakly perennial grasses (*Cynodon incompletus*) and herbs (*Abutilon sonneratianum* and *Protasparagus* spp.). Differential species include *Maytenus polyacantha, Pappea capensis* and *Rhigozum obovatum* as woody single- and multi-stemmed individuals. Soils have an organically-rich orthic-A horizon, varying in depth from 20-30 cm. Na levels are low, with a moderately acidic pH (Palmer 1988c).

P. afra may form a "curtain" around the perimeter of a number of individuals, creating a domed clump. This structure provides optimum foraging surface for the browsing herbivores. Excessively browsed examples (intensive agricultural use) do not display this "curtain" of vegetative material, but a suitable "rest" from intensive utilization has resulted in the development of this phenomenon the KNR (Palmer 1988a) and the Andries Vosloo Kudu Reserve (Palmer 1981).

IVA2 *Maytenus polyacantha-Pappea capensis* Degraded Succulent Thicket

Differential species (Table 9) include *Pappea capensis, Rhigozum obovatum, Carissa haematocarpa, Maytenus polyacantha* and *Boscia oleoides* (Figure 21). *Portulacaria afra* is absent. The presence of *Aristida diffusa, Protasparagus suaveolens, Enneapogon scoparius* and *Blepharis villosa* as differential species suggest that this is a degraded form of the Succulent Thicket.

The absence of *Portulacaria afra* may be a product of recent agricultural practices in the region. Repeated defoliation of *P. afra* causes mortality in this species (Aucamp 1979) and can result in fence-line contrasts (Figure 22). This destruction of the *P. afra* in the Succulent Thicket may be a result of the land-managers' persistence in ignoring the recommended 200 day re-foliation period (Aucamp 1979). *P. afra* is not a preferred browse species of domestic herbivores in Succulent Thicket containing *Boscia oleoides, Grewia robusta* or *Rhigozum obovatum* (Stuart-Hill pers. comm.). Utilization of the succulent shrub layer by domestic stock may reduce the total density from a potential 8718 to 696 shrubs per ha. (Stuart-Hill *et al.* 1986). *P. afra* does not display obvious anti-predator adaptation and recent sustained use has depleted the

Figure 22. A fenceline contrast in Roussouwspoort, with the degraded condition on the left and a conserved example on the right.

Table 9. A summary table of the differential and companion species of the Succulent Thicket of the Camdebo.

Class	IV		
Order	A		
Community	1	2	3
Number of relevés	10	13	5
Differential species of community IVA1			
Abutilon sonneratianum	2		
Panicum maximum	2		
Lycium oxycarpum	2		1
Rhoicissus tridentata	2		1
Schotia afra	1		1
Rhus refracta	1		
Diospyros austro-africana	1		
Viscum obscurum	1		
Crassula perforata	1		
Cussonia spicata	1		
Nymania capensis	1		
Cenchrus ciliaris	1	1	
Differential species of community IVA2			
Diospyros lycioides	1	4	
Protasparagus suaveolens	1	3	
Aristida diffusa	1	2	
Blepharis villosa		2	
Enneapogon scoparius		1	
Differential species of community IVA3			
Senecio longiflorus		1	5
Peliostomum origanoides	1		5
Aizoon rigidum	1		5
Pachypodium succulentum		1	3
Lycium schizocalyx	1		3
Aloe striata			1
Galenia sarcophylla			1
Euphorbia heptagona			1
Differential species of communities IVA1, 2 & 3			
Portulacaria afra	5		5
Pappea capensis	4	3	3
Rhigozum obovatum	3	4	5
Carissa haematocarpa	3	3	
Aristida congesta	2	3	1
Maytenus polyacantha	5	5	1
Boscia oleoides	1	3	
Protasparagus striatus	1	3	1
Crassula ovata	1		1
Aloe ferox	2	4	1
Companion species			
Pentzia incana	5	5	5
Grewia robusta	4	5	5
Rhus longispina	2	1	
Acacia karroo	3		
Eragrostis obtusa	1	1	
Chrysocoma ciliata	1	1	
Cynodon incompletus	1	1	
Euclea undulata	1	1	
Crassula muscosa	1		1

historical distribution. A comparison of Acocks' (1975) map (Figure 23) with the vegetation map prepared using satellite imagery (Figure 24), provides further evidence for a decline in the area covered by Succulent Thicket. The Succulent Thicket in Figure 8 includes both the transformed and untransformed communities.

IVA3 *Peliostomum origanoides-Portulacaria afra* Succulent Thicket

Located on the north-facing middle pediments, this community is encountered mainly on the KNR. Differential species are *Peliostomum origanoides, Aloe striata, Lycium schizocalyx, Aizoon rigidum* and *Euphorbia heptagona*. High cover-abundance values for *Rhigozum obovatum* and *Grewia robusta* are recorded and dolerite boulders are consistently present. Mudstone was occassionally present in the geological material in the relevés, suggesting this community is associated with these mineralized soils.

V Riparian Thicket

VA *Lycium oxycarpum-Maytenus heterophylla* Riparian Thicket

The Dwarf Shrublands are broken by the rivers and streams which drain the plains, and provide moisture regimes suitable for the development of Riparian Thicket (Table 10). The constituent species are woody shrubs and trees, including *Ziziphus mucronata, Maytenus heterophylla, Acacia karroo, Olea europaea* and *Diospyros lycioides*. The herb layer consists of both grass and dwarf shrubs. The species in this community show both Sub-Tropical and Sudano-Zambezian affinity, suggesting that this habitat may represent refuges for woody species in this semi-arid environment. I did not sample this community intensively and refrain from providing more information than Werger (1980).

Synonymy: *sensu stricto* Zizipho-Acacietum karroo (Werger 1980).

Table 10. A summary table of the differential and companion species of the Riparian Thicket of the Camdebo.

Class	V
Order	A
Community	1
Number of relevés	5
Differential species of community VA1	
Ehretia rigida	2
Grewia occidentalis	2
Grewia robusta	2
Rhus pentherii	1
Melolobium candicans	1
Chloris virgata	1
Ziziphus mucronata	1
Diospyros lycioides	1
Maytenus heterophylla	1
Azima tetracantha	1
Cussonia spicata	1
Walafrida geniculata	1
Olea europaea	1
Companion species	
Cynodon incompletus	5
Acacia karroo	4
Protasparagus striatus	3
Pentzia incana	3
Aristida congesta	2
Tribulus terrestris	2
Atriplex lindyeii	2
Infrequent species	
Lycium oxycarpum	1
Euclea undulata	1
Lepidium africanum	1
Lycium schizocalyx	1
Blepharis capensis	1
Walafrida geniculata	1
Indigofera denudata	1
Eragrostis obtusa	1
Pappea capensis	1
Rhus longispina	1
Boscia oleoides	1
Juncus effusus	1
Salsola kali	1
Pachypodium succulentum	1
Senecio burchelli	1
Melolobium candicans	1
Crassula muscosa	1
Salsola aphylla	1
Barleria obtusa	1
Circium vulgare	1
Eragrostis lehmanniana	1

4.0 DISCUSSION AND CONCLUSION

The development of concepts of ecosystem structure (community unit, individualistic, multiple working hypothesis) have emphasized the danger of over-simplifying ecosystem structure by interpreting gradients using restricted environmental data. I confine the interpretation of the classification achieved in this study to the precipitation gradient.

The rainfall isohyets (Figure 7) provide better differentiation of precipitation nodes than those published for the study area (Venter *et al.* 1986). The nodes of low rainfall (<250mm per annum) co-incide with the incidence of Succulent Dwarf Shrubland, and the high rainfall co-incide with Grassland and Forest (>400mm), with the Grassy Dwarf Shrubland occurring in the interval from 250-350mm per annum. This relationship between the rainfall pattern and vegetation suggests that precipitation is an important environmental factor contributing to the distribution of the flora.

The long-term precipitation records (Figure 8) for the eastern Cape indicate an oscillation about a mean with protracted periods (80 years) between "wet" pulses. This period extends from circa 1893 to 1974. Extreme dryness was a feature during the early part of this century when many agricultural policies and theories on karoo vegetation dynamics were being prepared. Mentis (pers. comm.) suggests that the arid components of the system may be driven by pulses of precipitation or disturbance.

In the Dwarf Shrubland, a vegetation mosaic exists, each stand possibly representing a different age since last disturbance. Small mammal activity probably contributes to these disturbances. Prentice & Werger (1985) report that in a Succulent Dwarf Shrubland in Namaqualand, a pattern of aggregation caused by a regeneration is evident in young communities. As these communities decay, the distribution of individuals tends towards randomness as larger individuals compete with one another for resources (Prentice & Werger 1985). The application of different agricultural treatments, in the form of grazing regimes, may further disadvantage decaying communities resulting in a more rapid decline.

In the Sub-Tropical Transitional Thicket, the vegetation varies from succulent bushclumps to very dense thicket. Both types may be adjacent and it is impossible to differentiate them in Figure 9. Three theories are proposed to explain clumping in shrubland: opening up by stock of a formerly dense vegetation (*sensu* Acocks 1975); the retrogression of a formerly more extensive thicket as a result of fire and the promotion of fire-climax grassland (Martin & Noel

1960) or the colonization of Grassland or Dwarf Shrubland by Thicket and Shrubland precursors (Tinley 1975). All are pertinent to explaining clumping in woody and succulent elements of the bushclumps and thicket.

The boundaries of homogeneous stands of this order are detectable on LANDSAT imagery when spectral reflectance patterns dominated by high digital values in Band 7 are used in association with ground reference information (Palmer 1988d). The boundaries of the polygons were generally sharp, making the monitoring value of the MSS data invaluable. Transformation within the order has taken place in both the shrub component and the herbaceous layer, resulting in a range of associations.

Numerous low growing, multi-stemmed *Euphorbia* spp. have evolved sympatrically in the Sub-Tropical Transitional Thicket (*E.bothae, E. coerulescens, E. ledienii*). These species occur in syntaxonomically related communities and there may be some basis for using these species to define orders in the class.

Earlier descriptions of the Grasslands (Acocks 1975) are not elaborated on by this study. The quadrats surveyed confirm his classification, and a second approximation would be more appropriate under the aegis of the Grassland Biome Project.

Multivariate statistical analysis (Dixon *et al.* 1985; Cooley & Lohnes 1971, Orloci 1978) of ancillary environmental data, particularly the results of soil analysis, may be used to further understand ecosystem structure. Detailed information on certain soil surface conditions was collected from some quadrats, and this is discussed in a later paper (Palmer 1988c).

Coetzee (1983) suggests that in natural ecosystems it is possible to integrate the multiplicity of biotic and abiotic components into a "landscape" classification system. The "landscape" comprises a recurrent pattern of plant associations with its associated fauna and abiotic habitat. The habitat or "ecotope" is a distinct class of land defined by its macro-climate, terrain form and soil pattern; and may be suitably mapped at 1:250 000 scale (MacVicar *et al.* 1974). The ecotope within a region may have its own distinct vegetation, although natural vegetation is unlikely to be the primary component of the ecotope, and the same ecotope with its associated vegetation type may be found in several types of landscape (MacVicar *et al.* 1974). In this study I suggest that each LSU can be classified according to its biotic and abiotic attributes, based on well-researched classification schemes for all of these attributes. The floristic classification scheme achieved in this study provides the basis for this approach.

In order to incorporate the floristic classification into a broader regional perspective, I used an "expert system". Expert systems (or knowledge-based systems) are being applied in many areas of scientific decision making (O'Keeffe *et al.* 1987) and classification. Noble (1987) has discussed the application of expert systems to ecology, especially that part of ecology involved in the prediction of the consequences of human actions. The APES shell (Hammond & Sergot 1985) suited the requirements of this study and I developed an expert system-based classification procedure for LSU's (Palmer 1988g). I intend using ECOCLASS (Palmer 1988g) to model vegetation/environment interactions and prepare a set of tested working hypotheses.

A visual comparison between the summarized vegetation map for 3224 Graaff-Reinet (Figure 20) and the map of Acocks (Figure 19) reveals that VT42 and the Grassy Dwarf Shrublands of the Katberg Sandstones are similar in their location and extent. The Succulent Mountain Veld (VT 25) is more fragmented than suggested and the False Central Lower Karoo (synonymous with Succulent Dwarf Shrubland) extends further than was previously suggested (Acocks 1975). The Shrublands, with their Savanna/Grassland affinity (Palmer 1988f) deviate from the suggested Karoo affinity of the Karroid *Merxmuellera* Mountain Veld (VT 60).

To conclude, analysis of the floristic data using the Zürich-Montpellier approach has provided an hypotheses on the vegetation of the region. This hypothesis can be further tested by:

i) applying the concepts to the description of the vegetation of a small area, such as the Karoo Nature Reserve (Palmer 1988a); and

ii) using ordination procedures to further understand the plant/environment interactions (Palmer 1988c).

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3224 Graaff Reinet

Veld Types (Acocks 1975)

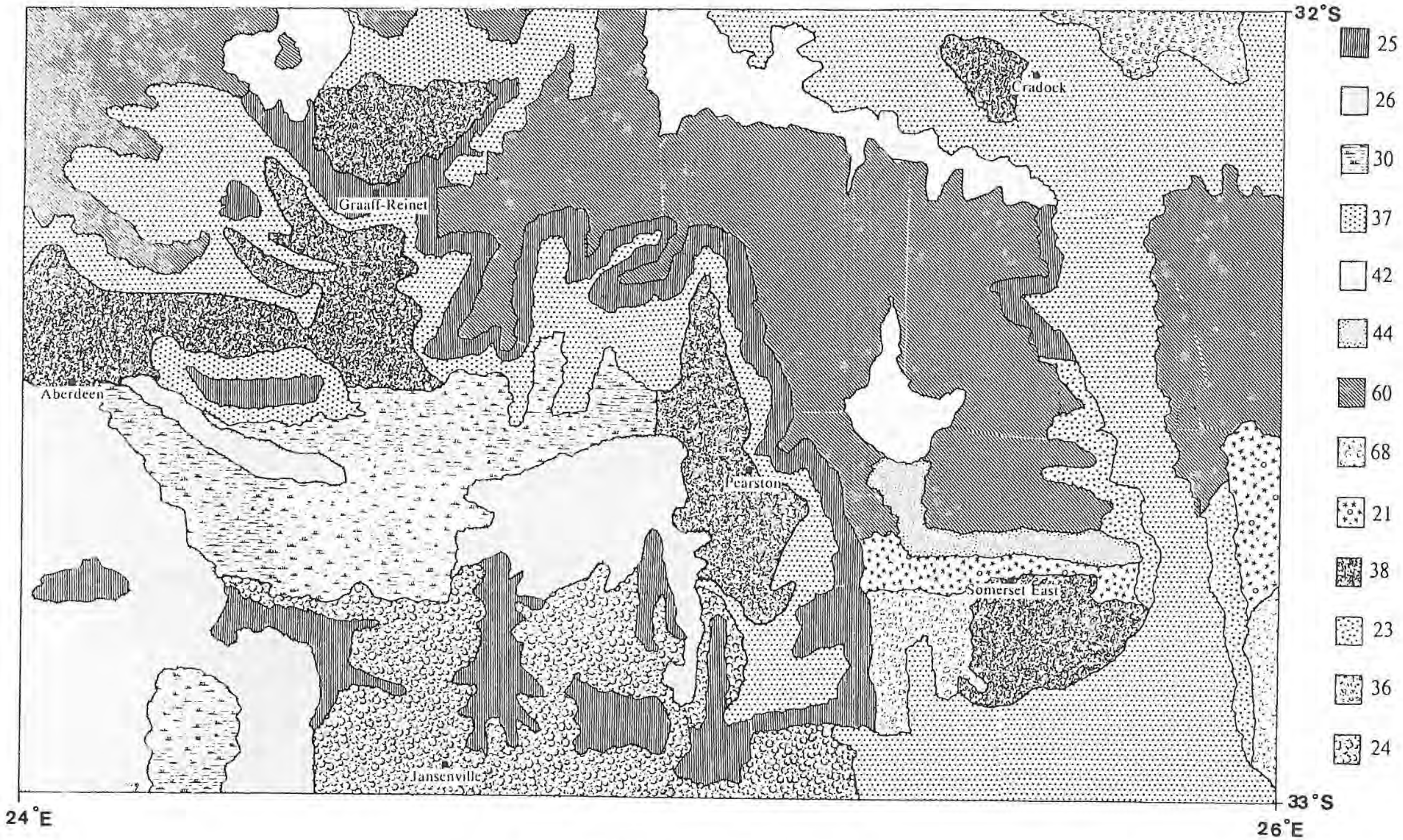

Figure 23. Acocks Veld Types for 3224 Graaff-Reinet.

3224 GRAAFF-REINET VEGETATION

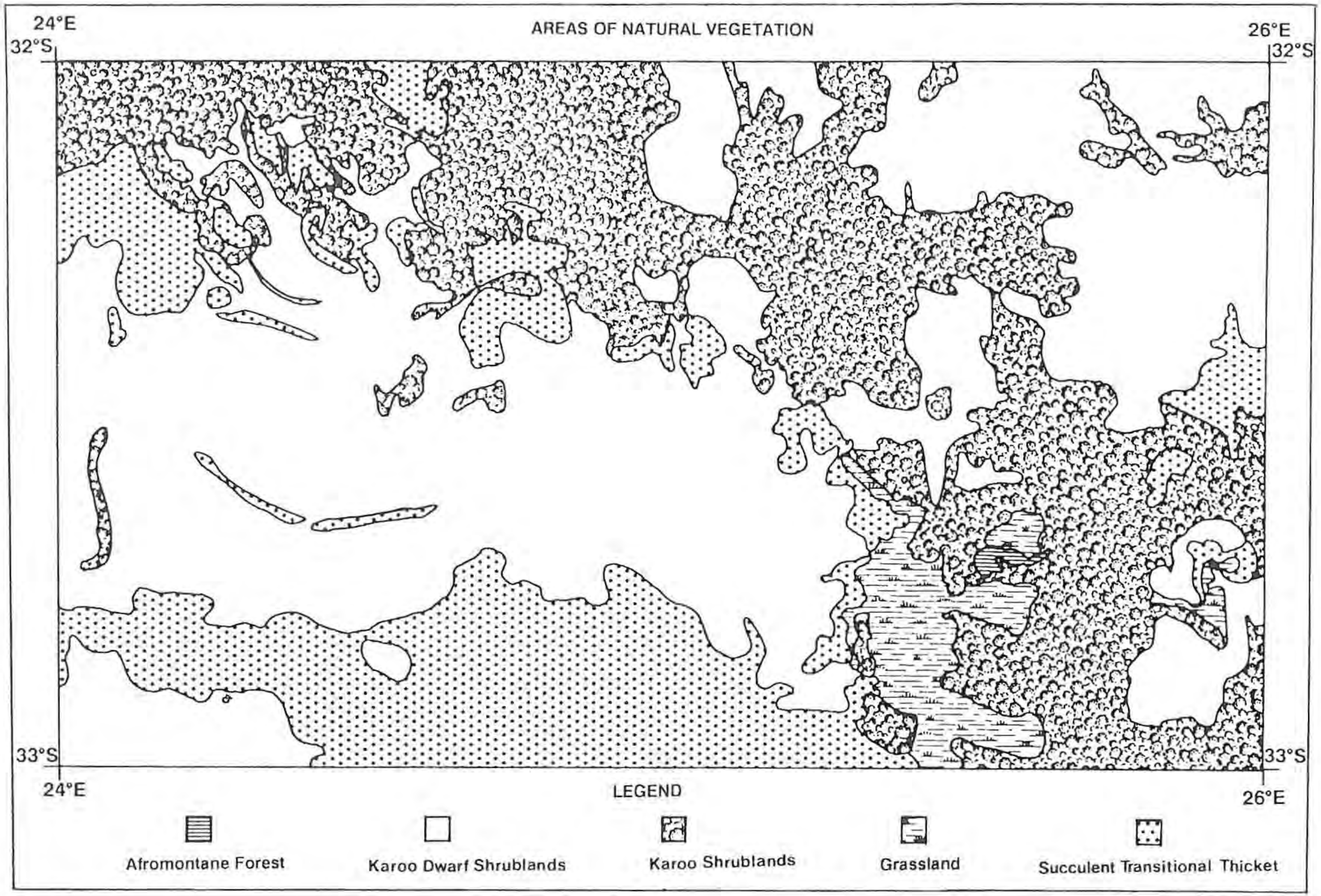

Figure 24. The vegetation map for 3224 Graaff-Reinet.

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APPENDIX 1

List of codes for the taxa represented in Figure 9.

CYMB MAR	*Cymbopogon marginatus* (Steud.) Stapf ex Burtt Davy
CYMB PLU	*Cymbopogon plurinodis* (Stapf) Stapf ex Burtt Davy
HETE CON	*Heteropogon contortus* (L.) Roem. & Schult.
THEM TRI	*Themeda triandra* Forssk.
DIGI ERI	*Digitaria eriantha* Steud.
PANI MAX	*Panicum maximum* Jacq.
SETA NEG	*Setaria sphacelata* (Schumach.) Moss var. *sphacelata*
ERHA CAL	*Ehrharta calycina* J.E.Sm. var. *angustifolia*
MERX DIS	*Merxmuellera disticha* (Nees) Conert
ARIS CON	*Aristida congesta* subsp. *congesta*
ARIS DIF	*Aristida diffusa* var. *burkei*
TRAG KOE	*Tragus koeleroides* Aschers.
SPOR FIM	*Sporobolus fimbriatus* (Trin.) Nees var. *fimbriatus*
SPOR NIT	*Sporobolus nitens* Stent
SPOR LUD	*Sporobolus ludwigii* Hochst.
ERAG CUR	*Eragrostis curvula* (Schrad.) Nees
ERAG LEH	*Eragrostis lehmanniana* Nees var. *lehmanniana*
ERAG CUR	*Eragrostis obtusa* Munro ex Fical. & Hiern
MICR CAF	*Microchloa caffra* Nees
CYNO DAC	*Cynodon dactylon* (L.) Pers.
TETR DRE	*Tetrachne dregei* Nees
ENNA SCO	*Enneapogon scoparius* Stapf
HAWO VIS	*Haworthia viscosa* (L.) Haw.
ORNI SPP	*Ornithogalum* sp.
PROT SUA	*Protasparagus suaveolens* (Burch.) Oberm.
MOQI RUB	*Moquinella rubra* (Spreng.f.) Balle
EBER SPI	*Eberlanzia spinosa* (L.) Schwant.
MESE KAR	*Mesembryanthemum karrooense* L. Bol.
PSIL ABS	*Psilocaulon articulatum* (Thunb.) Schwant.
PORT AFR	*Portulacaria afra* Jacq.
DIAN NAM	*Dianthus namaensis* Schinz var. *namaensis*
ACAC KAR	*Acacia karroo* Hayne
EUPH COE	*Euphorbia coerulescens* Haw.
RHUS REF	*Rhus refracta* Eckl. & Zeyh.
RHUS LON	*Rhus longispina* Eckl. & Zeyh.
RHUS ERO	*Rhus erosa* Thunb.
MAYT POL	*Maytenus polyacantha* (Sond.) Marais
MAYT HET	*Maytenus heterophylla* (Eckl.& Zeyh.)
PAPP CAP	*Pappea capensis* Eckl. & Zeyh.
ZIZI MUC	*Ziziphus mucronata* Willd. subsp. *mucronata*
GREW ROB	*Grewia occidentalis* L.
GREW ROB	*Grewia robusta* Burch.
ABUT SON	*Abutilon sonneratianum* (Cav.) Sweet

Appendix 1 (continued)

HIBI PUS	*Hibiscus pusillus* Thunb.
GNID POL	*Gnidia polycephala* (C.A. Mey.) Gilg
GNID CUN	*Gnidia microphylla* Meisn.
PASS MON	*Passerina montana* Thoday
EUCL UND	*Euclea undulata* Thunb. var. *undulata*
DIOS AUS	*Diospyros austro-africana* De Winter
DIOS LYC	*Diospyros lycioides* Desf. subsp. *lycioides*
OLEA EUR	*Olea europaea* L.subsp.*africana*
BUDD SAL	*Buddleja saligna* Willd.
PACH SUC	*Pachypodium succulentum* (L.f.) Sweet
EHRE RIG	*Ehretia rigida* (Thunb.) Druce
LANT RUG	*Lantana rugosa* Thunb.
BECI BUR	*Becium burchellianum* (Benth.) N.E.Br.
LYCI CIN	*Lycium cinereum* Thunb.
LYCI OXY	*Lycium oxycarpum* Dun.
LYCI SCH	*Lycium schizocalyx* C.H. Wr.
APTO PRO	*Aptosimum procumbens* (Lehm.) var. *procumbens*
SUTE ATR	*Sutera atropurpurea* (Benth.) Hiern
RHIG OBO	*Rhigozum obovatum* Burch.
JUST CUN	*Justicia cuneata* Vahl subsp. *cuneata*
LIGH ALB	*Lightfootia albens* Spreng. ex A.DC.
PTER GLA	*Pteronia glauca* Thunb.
FELI MUR	*Felicia muricata* (Thunb.) Nees subsp. *muricata*
FELI FIL	*Felicia filifolia* (Vent.) Burtt Davy subsp. *filifolia*
FELI HYS	*Felicia hyssopifolia* (Berg.) Nees subsp. *polyphylla*
CHRY CIL	*Chrysocoma ciliata* L. (= *C. tenuifolia* Berg.)
HELI ROS	*Helichrysum rosum* (Berg.) Less. var. *rosum*
HELI NUD	*Helichrysum nudifolium* (L.) Nees
PEGO RET	*Pegolettia retrofracta* (Thunb.) Kies
ERIO AFR	*Eriocephalus africanus* L.
ERIO ERI	*Eriocephalus ericoides* (L.f.) Druce
PENT INC	*Pentzia incana* (Thunb.) Kuntze
SENE RAD	*Senecio radicans* (L.f.) Sch. Bip.
EURY TEN	*Euryops tenuissimus* (L.) DC. subsp. *tenuissimus*
EURY SPA	*Euryops spathaceus* DC.

The vegetation of the Karoo Nature Reserve, Cape Province
I. A phytosociological reconnaissance.

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ABSTRACT

A phytosociological survey according to the approach and methods of the Zürich-Montpellier school was carried out on the Karoo Nature Reserve, Graaff-Reinet, South Africa. The study area is 160 km^2 in extent, and climatically it falls within the semi-arid zone. The complex climatological, geological, soil, vegetation and land-use gradients are emphasized. Eleven natural plant communities are recognized, reflecting a gradient from the warm, xeric conditions of the pediments to the cool, mesic conditions of the mountain ridges and plateaux. An hierarchical classification of the communities has been prepared, with the first division, corresponding roughly to the level of order, dividing the vegetation into Shrubland, Succulent Thicket and Dwarf Shrubland. The Shrubland is further divided into Open Shrubland on rocky slopes, Open Shrubland on dolerite upland and Grassy Open Shrubland. The Dwarf Shrubland is divided into grassy, succulent and degraded forms.

UITTREKSEL

'n Fitososiologiese opname, waarin gebruik gemaak is van die benadering en metodiek van die Zürich-Montpellier skool, is uitgevoer in die Karoo Natuurreservaat, Graaff-Reinet, Suid-Afrika. Die klimaat is semi-aried en die studiegebied is 160 km^2 in oppervlakte. Die komplekse gradiënte in klimaat, geologiese struktuur, gronde, plantegroei en bodembenutting word beklemtoon. Elf natuurlike plantgemeenskappe, wat die gradiënt van die warm, droë toestande van die vlaktes na die koel, klam toestande van die bergrante en platos, word beskryf. 'n Hierargiese klassifikasie van die gemeenskappe is voorberei. Die eerste skeiding, wat min of meer met die vlak van orde ooreenstem, het die plantegroei in Struikveld, Sukkulente Bosveld and Dwergstruikveld ingedeel. Die Struikveld is verder in Ope Struikveld van die klipperige Randjies, Ope Struikveld van die Doleriet hoogland en Grasagtige Ope Struikveld onderverdeel. Die Dwergstruikveld is in grasagtige, sukkulente en versteurde vorms ingedeel.

Keywords: semi-arid, Dwarf Shrublands, Shrublands, Succulent Thicket

INTRODUCTION

The Karoo Nature Reserve (KNR) was established on land surrounding the town of Graaff-Reinet, Cape Province, in 1976. The project to purchase the land was initiated by the South African Nature Foundation in an effort to conserve the ecological and cultural historic aspects of the region. The land set aside for conservation in this project was officially donated to the Cape Department of Nature and Environmental Conservation (CDNEC) on 24 August 1979. After establishment, the management of the nature reserve had to be planned in accordance with objectives agreed to by the Director of Nature and Environmental Conservation, namely the "conservation and scientific management of a representative example of a karoo ecosystem for the maintenance of genetic diversity and continuity of all natural elements in the ecosystem". This planning necessitated the accumulation of comprehensive natural resource data and the synthesis of these data to provide a statement on the ecological status of the area. The plant community is the fundamental unit of a terrestrial ecosystem and an understanding of the plant-environment relationship is the basis of any terrestrial ecosystem management policy. Plant community composition and distribution is directly related to environmental characteristics (Huntley & Birks 1979), and suitable survey methods had to be selected to develop hypotheses on vegetation function. Werger (1973) suggests that if Braun-Blanquet phytosociological surveys are undertaken in all conservation areas within South Africa, the classification of plant communities at points distributed over a variety of veld types (Acocks 1975) would be achieved. This method would provide a classification of the vegetation into "ecological units correlated with stable and permanent conditions, distinguishing, therefore, areas of uniform potential for management purposes" (Coetzee 1974).

The objectives of this study were:

i) to prepare an inventory of the plant communities of the nature reserve;

ii) to classify these communities using the Braun-Blanquet technique;

iii) to relate selected environmental variables with the communities in an effort to provide management with a list of communities requiring rehabilitation.

THE STUDY AREA

The KNR is approximately 16 200 ha in extent, and surrounds the town of Graaff-Reinet (Figure 1). The altitude on the reserve varies from 805 m at the Sundays River to 1 565 m at Drie Koppe in the east. The study area extends from 32° 10' to 32° 20'S , and from 24° 28' to 24° 41' E, and is mapped on S.A. Topo Series sheets 3224 AB, AD, BA and BC.

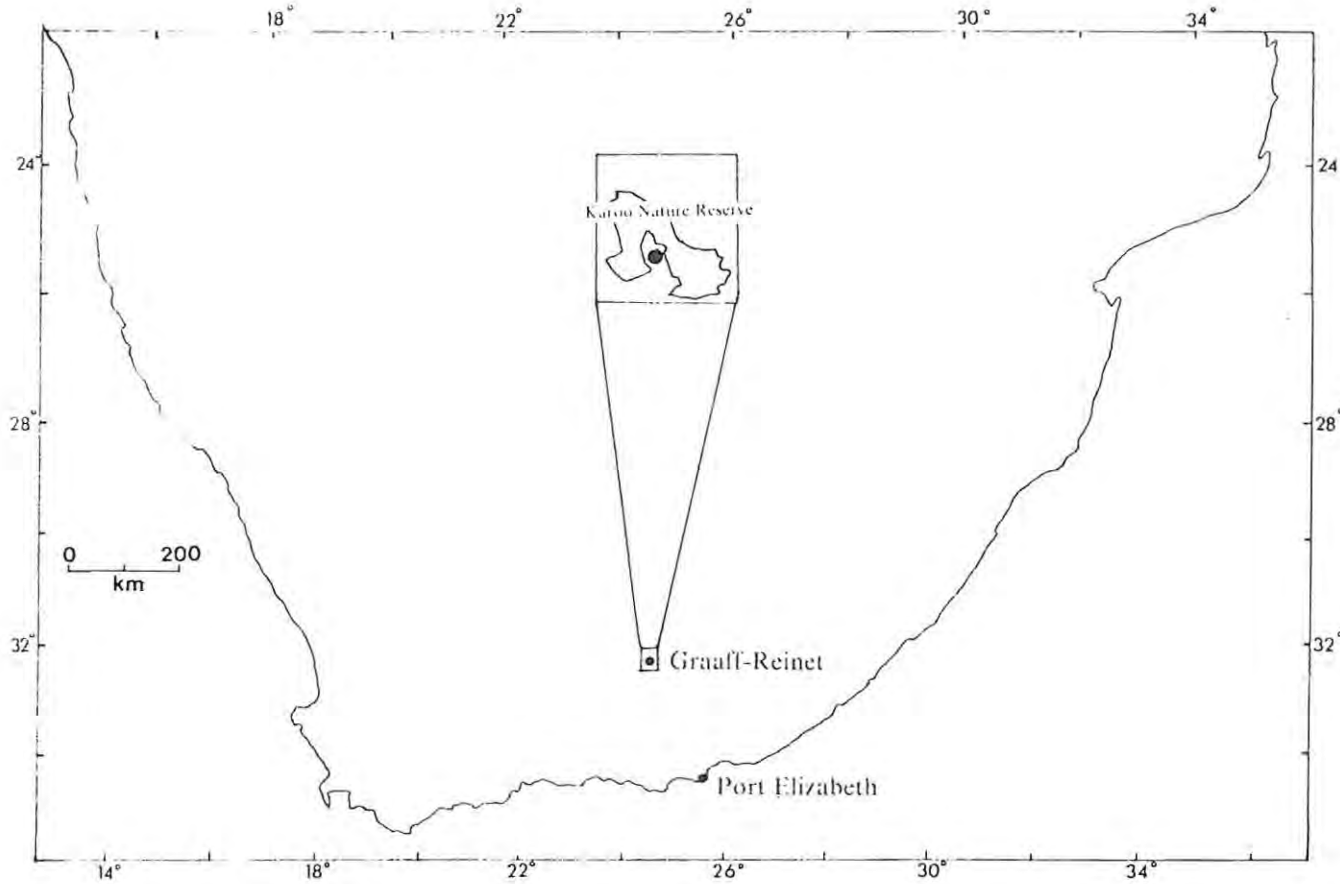

Figure 1. The location of the study area.

The nature reserve was formerly town commonage administered by the Graaff-Reinet municipality. During the last two hundred years, stock farmers and speculators have kept domestic stock (cattle, sheep, horses and goats) on the land. Natural populations of wild ungulates, which were recorded in the area when it was donated to the CDNEC, included kudu (*Tragelaphus strepsiceros*), grey duiker (*Sylvicapra grimmia*), mountain reedbuck (*Redunca fulvorufula*), steenbok (*Raphicerus campestris*), klipspringer (*Oreotragus oreotragus*) and numerous species of small mammal. The inaccessibility of much of the area to vehicles, the limited natural and artificial water points, as well as the large size of the camps, resulted in extremely poor veld management, with continuous grazing being a common practice. Description of the vegetation in this study must be seen in the light of this agro-ecological history.

With the advent of the biome approach to describing the vegetation of southern Africa, Werger (1978) and White (1983) prefer to regard the extensive arid and semi-arid areas of the south-western part of southern Africa as the Karoo-Namib biogeographical region. This region has subsequently been divided into three biomes by Rutherford & Westfall (1986), namely Nama-Karoo Biome, Succulent Karoo Biome and Desert Biome. The study site is situated at the eastern extremity of the Nama-Karoo Biome.

Physiography

The KNR forms part of the southern portion of the Karoo Mountain Veld Complex, which is in turn part of the Great Escarpment (King 1942). The mountains are represented by the peaks Spandaukop (1 316 m), Valley of Desolation (1 399 m) and the three peaks of the Drie Koppe, with the highest being 1 565 m.

The northern end of the Camdebo plain is situated within the KNR. This plain is a large basin which is sharply dissected by the Sundays River and its tributaries, the Voël, the Melk, the Klip and the Swart Rivers. The process of pediplanation is still in a very active phase, with many non-perennial streams occurring.

Geology

The landscape of the reserve was developed on the Adelaide Subgroup of the Beaufort Group (Karoo Supergroup). The geological system consists of very thick layers of near horizontal strata of sedimentary rocks (Johnson & Keyser 1976). It is characterized by strong sandstone layers separated from one another by thick shale and mudstone, red-purple to grey and grey-green in colour. This sandstone is generally rich in feldspar which is easily eroded under current climatic conditions, while the shales and mudstones are relatively unstable and erode chemically and mechanically. Plateau and gulley erosion can be seen on the talus slopes and pediments. The material originating from this weathering process and the erosion process is usually clayey and rich in alkaline salts (Van Riet & Minnaar 1977).

The Adelaide Subgroup is further divided into the Balfour and Middelton Formations, the former consisting of grey mudstone, shale and sandstone, and the latter of grey and 'red' mudstone and sandstone (Johnson & Keyser 1976). The Middelton Formation is further divisible into the Graaff-Reinet Formation, and the largest parts of the southern pediments and the lower slopes of the mountains on the KNR consist of representatives of this formation, which consists of sandstone lenses with red and blue-green mudstones. The sandstone is fine to medium grained with a speckled appearance. The Graaff-Reinet Formation is covered by Quaternary alluvium and soil, with calcrete being present. This takes the form of carbonate-rich nodules and lenses, which probably represent palaeosols (Visser 1986).

The sedimentary deposits are intruded by Stormberg (Karoo) dolerites to form sills and dykes. The dolerites consist predominantly of sills which can vary in thickness from less than a metre to 300 m (Visser 1986). The dykes cut across the bedding, and may be up to 10 m wide, with individual dykes being followed for 85 km (Truswell 1977) in other parts of the region. The dolerite intrusions affect the adjacent mudstone, siltstone and sandstone, creating metamorphic rocks such as lidianite from the mudstone (Visser 1986).

The largest part of the pediment is covered with alluvium, wash, gravel, sands, mud and wash stone of recent origin, with characteristic superficial calcrete (Figure 2). The alluvium may be as deep as 23m at some places (Johnson & Keyser 1976). These Tertiary to Quaternary deposits are an important feature influencing the vegetation of the Karoo biome, as they represent the growth medium for many dwarf shrubs in the region.

Soils

The soils of the study area have been briefly described and mapped (Figure 3) by Van Riet & Minnaar (1977). The soil mapping units recognized by these authors range from the shallow (< 20 cm) Mispah-rock complex, to the deep (> 120 cm), red brown calcareous duplex soils of the Shigalo-Limpopo Association. The Mispah-rock complex is associated with the dolerite sills and dykes which intrude the sedimentary beds of the Beaufort Group. In general, the A-horizons of these shallow soils of pedologically young landscapes, are rich in most plant nutrients (Ellis & Lambrechts 1986), displaying orthic topsoil horizons. The presence of dolerite boulders overlying the basic soils of the pediments enhances soil quality by reducing alkalinity and improving the

Figure 2. The white calcareous hardpan in a soil profile on the Karoo Nature Reserve. The hardpan is encountered at approximately 30 cm below the surface of the pediments throughout the Camdebo plain. Roots, obvious in the upper half of the photograph, are seldom found below this layer.

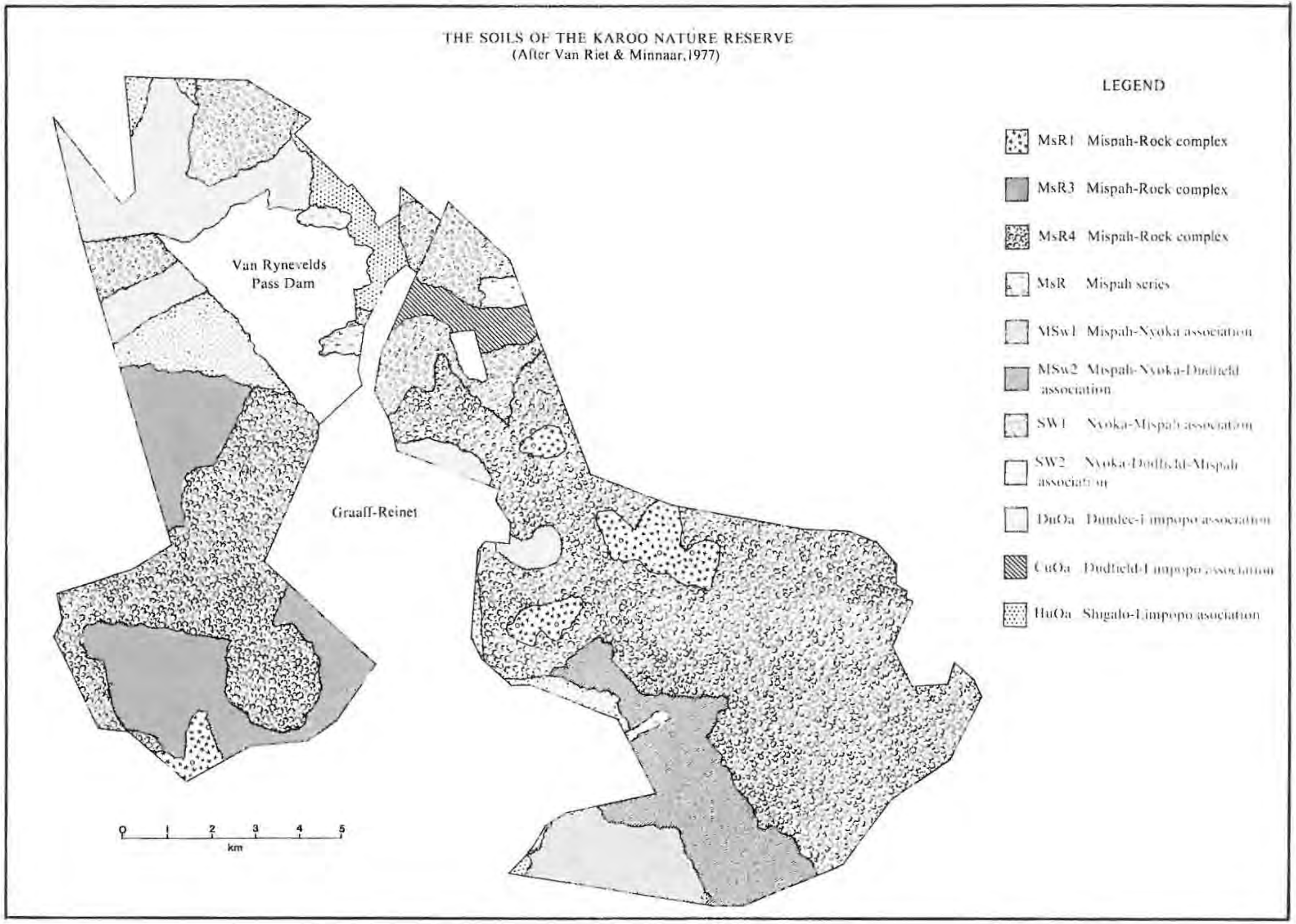

Figure 3. The soils of the Karoo Nature Reserve (after Van Riet & Minnaar 1977).

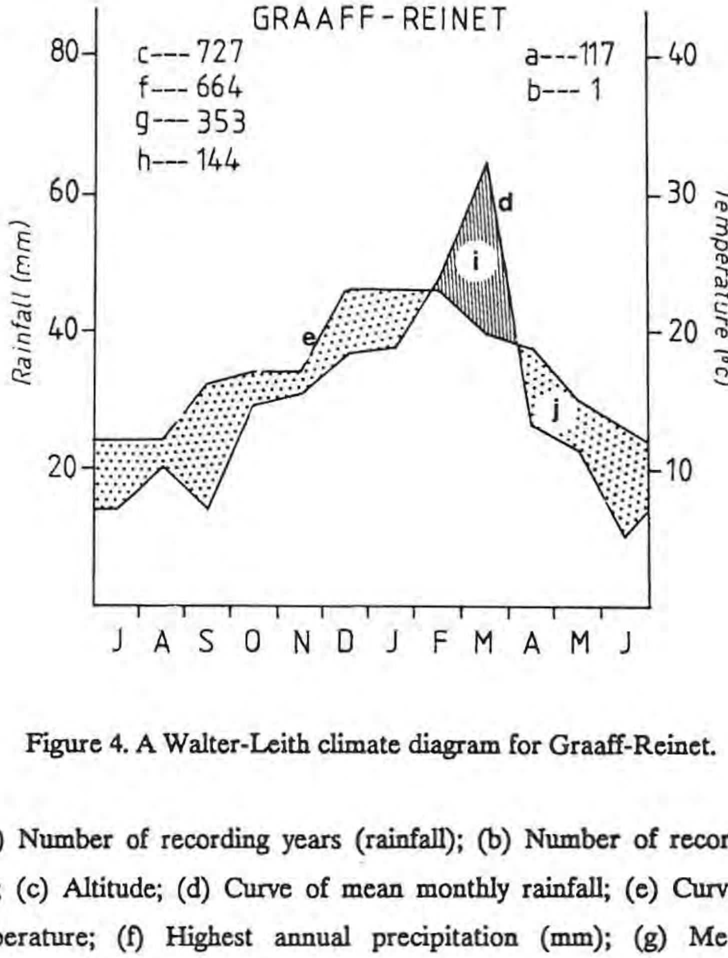

Figure 4. A Walter-Leith climate diagram for Graaff-Reinet.

LEGEND. (a) Number of recording years (rainfall); (b) Number of recording years (temperature); (c) Altitude; (d) Curve of mean monthly rainfall; (e) Curve of mean monthly temperature; (f) Highest annual precipitation (mm); (g) Mean annual precipitation (mm); (h) Lowest annual precipitation (mm); (i) Wet season; (j) Dry season.

water-holding capacity. Improved protection afforded by vegetation (mainly mesophytic species) reduces erosion.

The pediment soils are red, apedal, weakly structured, freely drained soils with a high base status (Ellis & Lambrechts 1986). The soils are generally calcareous duplex forms of a secondary nature, having been deposited as alluvium on the impermeable sandstone. These duplex soils are subject to sheet and gully erosion, which is aggravated by a reduction in vegetative cover.

Climate

Some of the oldest meteorological stations in southern Africa are located in or near the study area, with rainfall records for Graaff-Reinet from 1861 and Grahamstown from 1865 being well preserved (Tyson 1986). The general description is of a semi-arid climate, with 32% of the rain falling during the hottest months of the year (February-April) (Figure 4). Fogs occur frequently over the high-lying areas, predominantly from February to April, and contribute to moisture availability in these areas. Frost is usually experienced from April to September, and snow is a regular winter feature of the high-lying plateaux. Maximum air temperatures during summer may exceed 43°C, with winter minima falling below -3°C on occasions. Although there is no evidence for a progressive desiccation at Graaff-Reinet in the period of the meteorological record, oscillatory variations in the rainfall are apparent (Tyson 1986).

MATERIALS AND METHODS

Sampling strategy

Stratified random sampling (Southwood 1978) employs the principle that an initial classification of the study area is carried out during which the study area is divided into reasonably homogeneous units. The boundaries of twelve homogeneous cover classes were recognized from a Landsat image, which was recorded over the study area on 8 November 1980 (Scene ID 22117-07312 WRS 184-82), using the technique described by Harrington & Dunn (1980). Quadrats were selected at random within each of the cover classes, and surveyed using the Zürich-Montpellier phytosociological approach and methodology (Werger 1974). Seventy-eight quadrats measuring 10 m x 10 m were selected throughout the study area (Figure 5). A plot size of 10 m x 10 m has been used in the fynbos and Afro-montane forest in the south-western Cape (Werger *et al.* 1972; McKenzie *et al.* 1977; McKenzie 1978) and in the Succulent Thicket of the Great Fish River (Palmer 1981). Some researchers in the fynbos have used a smaller plot (10 m x 5 m) (Taylor 1969; Bond 1981). Nested quadrats containing plot sizes 1, 5, 10, 100 and 200 m^2 (see Whittaker *et al.* 1979) were sampled in a range of vegetation types in and adjacent to the study area, and the 10 m x

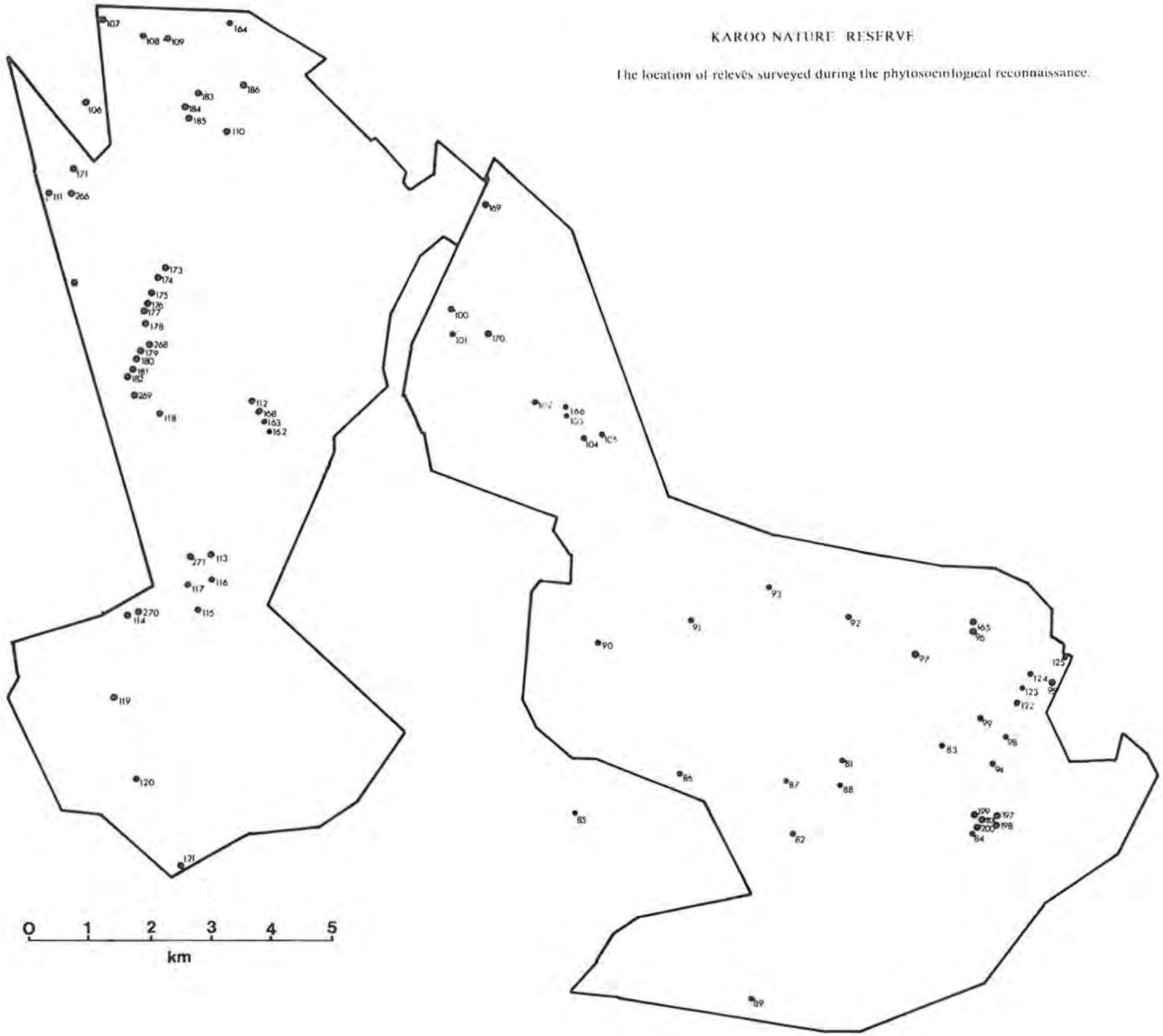

Figure 5. The distribution of relevés surveyed on the Karoo Nature Reserve.

10 m plot yielded the desired level of information (>50%). This size was considered optimal for all vegetation in the study area. Total floristic information was collected from each of the quadrats, together with information on aspect, slope, geology, physiography, soils and other biotic influences. All plant specimens collected were submitted to the National Herbarium, Pretoria, for identification, and a reference collection was established and is housed on the KNR (Palmer 1988a). The cover-abundance values applied were those recommended by Barkman *et al.* (1964). Re-arrangement of the data followed a manual tabulation technique in which columns and rows of data in the matrix are arranged using a micro-processor (Palmer & Lubke 1982). TWINSPAN (Hill 1979, Gauch 1982) was used to provide an initial classification of the data.

RESULTS

A summary table of the plant communities of the KNR is presented (Table 1). Each quadrat is represented by a column in the table, with quadrat numbers appearing at the top. The vegetation of the KNR can at present be divided into eleven natural plant communities representing the Karoo-Namib and Tongaland-Pondoland phytogeographical regions. No excessively disturbed or specialized components such as littoral fringes, vleis or river bank communities were sampled.

A hierarchical presentation of the TWINSPAN classification (Figure 6) facilitates the description. The aridity gradient from Grassy Shrubland to Succulent Dwarf Shrubland was differentiated using both data manipulation techniques.

A vegetation map (Figure 7) was produced by classifying each of the homogeneous vegetation sampling units into one or other of the vegetation categories. Many of the assumptions associated with vegetation classification and mapping (Shipley & Keddy 1987) have been taken into consideration during this study. I have attempted to cover the broad conceptual elements of the vegetation (Figure 7), which are described in detail below, without trying to delineate specific boundaries, except where these represent sharp contrasts between physiognomically distinct units.

Interpretation of the TWINSPAN hierarchical classification (Figure 6) reveals that three formations are recognized at levels one and two. These are Shrubland, Succulent Thicket and Dwarf Shrubland of the rocky and sandy soils.

SHRUBLAND

The Shrubland (*sensu lato* False Karroid Broken Veld (Acocks 1975); scrub (Werger 1980)) occurs predominantly on uplands with sandstone and dolerite parent material. The most prominent structural feature is the presence of scattered bush clumps, each of which may contain fifteen or

Table 1. A synoptic table of the differential species of the plant communities of the Karoo Nature Reserve. The numerals are ratings of constancy based on a five point scale: 1 = 1 to 20%; 2 = 21 to 40%; 3 = 41 to 60%; 4 = 61 to 80% and 5 = 81 to 100% constancy.

Community Number	A	B	C	D	E	F	G	H	I	J	K
Number of relevés	9	2	3	5	3	5	15	8	2	11	11
Differential species of the Shrublands (communities A,B,C,D,E & F)											
Rhus undulata var. *undulata*	4	5	5	5	2	1	1				
Euryops spathaceus	2	3	5		2	4					
Walafrida geniculata	2		4		2	1					
Ehrharta calycina	2		3	4	4	1					
Aloe broomii var. *tarkaensis*	3										
Buddleja saligna		3	2	2		1					
Olea europaea subsp. *africana*		3	2								
Euclea undulata	2				3	2	1				
Maytenus polyacantha	2		1		1	1	3				
Eragrostis chloromelas					5						
Differential species of the Open Shrubland on dolerite upland (communities D & E)											
Heteropogon contortus				3			1				
Digitaria eriantha			2	4							
Cymbopogon plurinodis				3		3	1				
Hibiscus pusillus	2		2	5	4	1					
Themeda triandra				5	5	4					
Sporobolus fimbriatus					4						
Lantana rugosa				3	1						
Grewia occidentalis		3		5	1						
Diospyros austro-africana			4	3	2	3	3				
Becium burchellianum	1					1	1				
Differential species of the Grassy Open Shrubland on rocky slopes (community E & F)											
Rhus erosa					4	3	1				
Merxmuellera disticha						1		1			
Mestoklema tuberosum					2	2					
Felicia hyssopifolia					1						
Sutera mollis				1			1				

Table 1 (continued)

Community Number	A	B	C	D	E	F	G	H	I	J	K
Differential species of the Succulent Thicket (community G)											
Pappea capensis							5				
Portulacaria afra							5				
Carissa haematocarpa							2				
Rhus refracta							1				
Aloe ferox	1						2				
Boscia oleoides							2				
Peliostomum origanoides							3				
Rhoicissus tridentata							1				
Panicum maximum							2				
Crassula ovata							1				
Indigofera heterophylla							1				
Sporobolus nitens							1				
Ehretia rigida	1						1	1			
Grewia robusta	3	1					5	1			
Rhus longispina	2			1			1				
Rhigozum obovatum							4			3	2
Differential species of the Dwarf Shrublands (communities H,I,J,K)											
Felicia muricata						1	1	2	2	1	2
Eragrostis obtusa				1	2		1	1	2	3	1
Aristida congesta				1			2	4	5	5	4
Protasparagus suaveolens	1			1	1				1	3	1
Senecio radicans	1				1					3	1
Rosenia humulis						1			3	3	3
Sutera halimifolia					1		1			2	
Differential species of the Succulent Dwarf Shrublands (community J)											
Pachypodium succulentum							1	1		3	2
Blepharis capensis				1			1	1		1	
Cadaba aphylla							1	1		1	1
Thesium rigidum							1			1	3
Salsola aphylla								1		1	
Differential species of the Succulent Dwarf Shrublands (communities J & K)											
Bulbine abyssinica										1	1
Eberlanzia spinosa										2	3
Polygala hottentotta										1	1
Haworthia viscosa										2	2
Eriocephalus africanus										1	1
Anacampseros telephiastrum										1	1
Senecio acutifolius										1	3
Trichodiadema pygmaeum										2	4
Pegolettia retrofracta										1	2
Senecio longiflorus							2			1	1
Euryops anthemoides subsp. *astrotrichus*										2	
Protasparagus acocksii							1			1	1
Sarcocaulon camdeboense										1	2
Felicia filifolia										1	1

Table 1 (continued)

Community Number	A	B	C	D	E	F	G	H	I	J	K
Differential species of the Succulent Dwarf Shrubland (community K)											
Lepidium divaricatum											1
Zygophyllum retrofractum											1
Galenia sarcophylla							1				5
Mesembryanthemum karrooense											2
Aptosimum procumbens											2
Psilocaulon articulatum											2
Companion species											
Pentzia incana	5	5	5	5		2	5	5	5	5	5
Chrysocoma ciliata	2	5	4	3	4	3	1	1	5	2	1
Eragrostis lehmanniana	1				5	3	1	3	3	3	
Helichrysum rosum var. *arcuatum*	2				1	2	1		1	1	1
Tragus koeleroides	1			5	4		1	1		4	
Eriocephalus ericoides	1			4	1					4	3
Blepharis villosa	1		3	5	1	1				4	4
Acacia karroo	3			4	2		2	1		1	
Lycium schizocalyx				4			1	1			5
Solanum tomentosum	1				2	1	1				
Aristida diffusa	1			2		1	1		1	1	
Crassula muscosa	1				1	1	2	1		2	2
Protasparagus striatus	1	1		1			2	1		1	1
Cynodon incompletus	2						1	2			
Hermannia althaeoides	2	3		1			1				

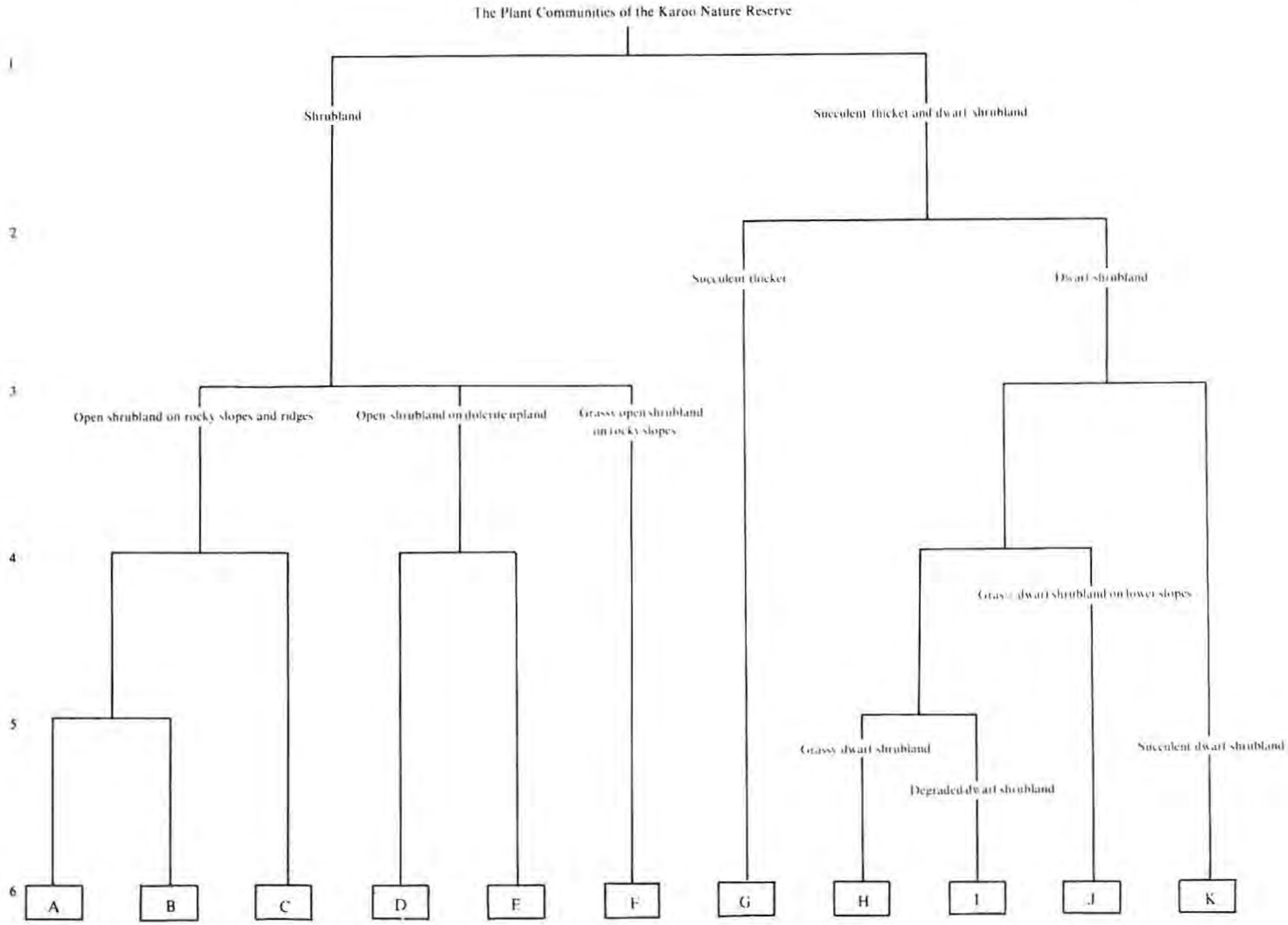

Figure 6. The hierarchical classification of the vegetation of the Karoo Nature Reserve. This was achieved after slight modification of the result of a TWINSPAN tabulation.

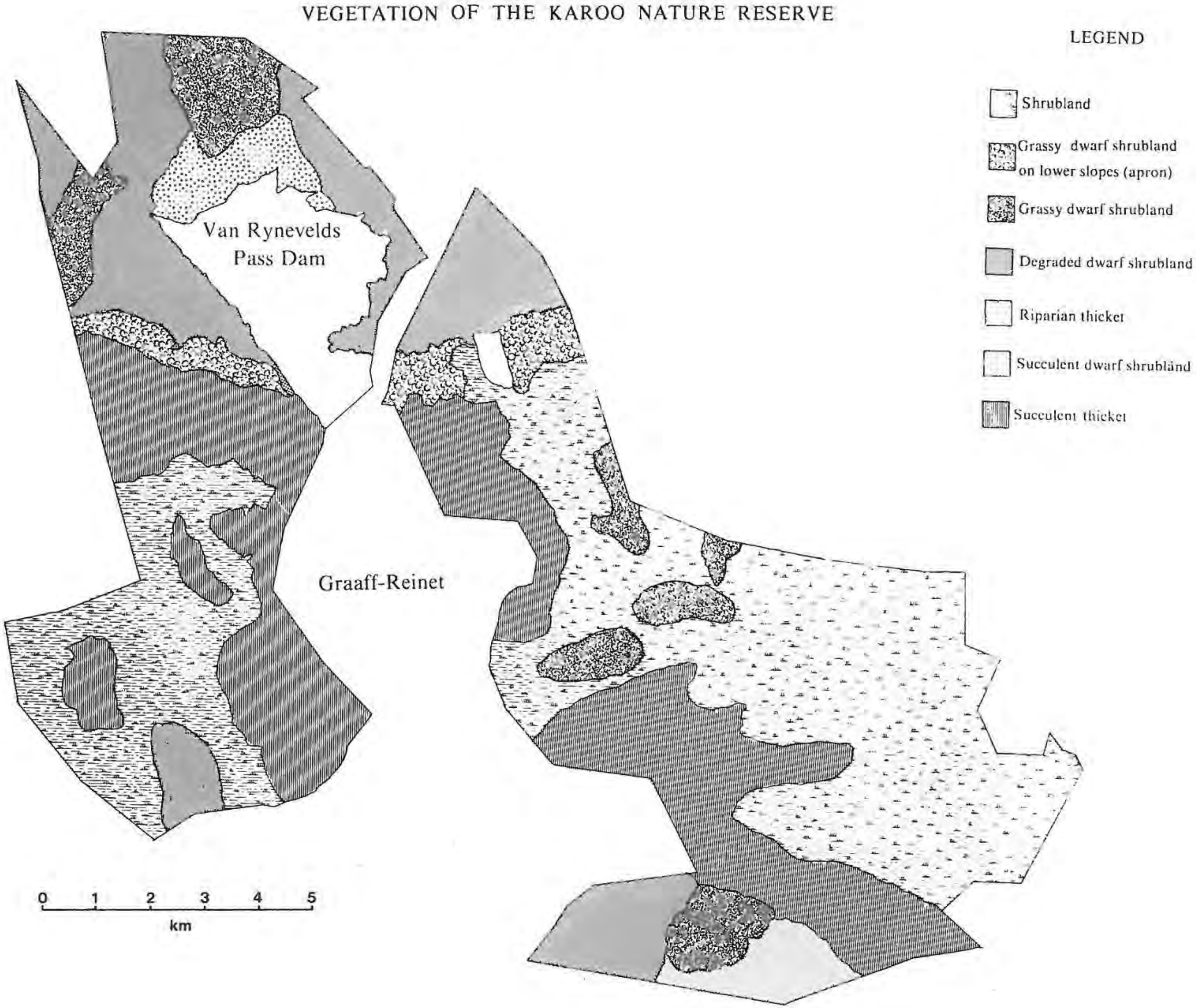

Figure 7. The vegetation map of the Karoo Nature Reserve.

Figure 8. The Shrublands of the rocky slopes and ridges of the Karoo Nature Reserve. Shrublands consist of clumps of woody species, *Rhus undulata, Maytenus polyacantha, Euclea undulata* and *Acacia karroo*, interspersed by Dwarf Shrubland or Grassland.

Figure 9. Open Grassy Shrubland on dolerite, with *Merxmuellera disticha, Themeda triandra* and *Rhus erosa*.

more species. This phenomenon has been recorded previously by Martin & Noel (1960) in the Albany and Bathurst districts and Palmer (1981) in the sub-tropical thicket of the Great Fish River valley. Edwards (1983) recommends the term "tall open shrubland" where shrub canopy cover is between 1 and 10%, and shrub height is from 1 to 2 m. However, the relative term "tall" does not describe the situation when viewed in relation to the "Dwarf Shrubland" of the pediments. I therefore propose to omit the height descriptor and concentrate on the aspect of shrub density, namely "open" referring to shrub density from 1-10%. Similarly the grassy component is not catered for in this descriptive vocabulary, and I propose to use the term "grassy" to describe the interclump cover. When dwarf shrubs are the dominant interclump growth form then specific mention will be made of this in the description.

The Shrubland is characterized by clumps of multi-stemmed woody shrubs, dominated usually by species of the genera *Rhus, Euclea, Maytenus, Olea, Buddleja, Grewia, Diospyros* and *Acacia*. It can be sub-divided into three variations (Figure 6): Shrubland of the rocky slopes and ridges, Open Shrubland on dolerite upland, and Grassy Open Shrubland. The two former variations are characterized by dwarf shrubs dominating the inter-clump cover, whereas the latter contains a greater abundance of grass, indicating a more mesic condition.

Shrubland of the rocky slopes and ridges

This variation is represented by three communities (A, B and C) situated between 1000 and 1300 m above sea level. The soils are part of the Mispah-rock complex in which a shallow (20-60cm) A-horizon covers rocky parent material. Large rocks and boulders (dolerite and lidianite) occur in the soil profile, and lead to an under-estimate of soil depth. The soils are deeper than expected, and woody shrubs can penetrate to a depth of 3 or 4 metres. This was evidenced by visible root penetration in cutting and gullies.

The most prominent shrub is *Rhus undulata* which occurs in all the quadrats in this variation (Figure 8). Other differential shrubs include *Maytenus polyacantha, Rhus longispina, Lycium oxycarpum, Ehretia rigida, Grewia robusta, G. occidentalis, Buddleja saligna* and *Olea europaea* susp. *africana*. The mean shrub canopy cover in the 100 m^2 quadrats was 28% (ranging from 10-60%), and varies in height from 1,5 to 3,0 m. This is lower when determined over the entire landscape, hence my acceptance of the Edwards' (1983) definition of "open" to describe the formation. Total canopy cover in the quadrats was moderately high (62%) with a range from 45 - 80%. Rocks accounted for 15 - 20% of cover, with the remaining inter-clump area being covered by dwarf shrubs and sparse grass.

Dwarf shrubs include *Pentzia incana, Chrysocoma ciliata, Walafrida geniculata, Hermannia* spp., *Elytropappus rhinocerotis* and *Euryops spathaceus*. Many of these species are regarded as arid-tolerant species which have prevailed and increased on account of intensive grazing pressure on more palatable species. It is strongly suggested in the literature (Tidmarsh 1948, 1957, Acocks 1975) that the presence of these dwarf shrubs represents a transformed condition from the recent historical situation which was apparently more grassy. In support of this suggestion, classification resulted in these communities (A, B and C) at one end of the hierarchy, the other end of which contained a higher proportion of grasses.

Open Grassy Shrubland on dolerite upland

This variation (communities D and E) occurs in the heterogeneous soils of the Mispah-rock complex, where sandstone, dolerite, lidianite and mudstone have been mixed in varying proportions. Dolerite rocks form the major component of the substrate, and the topography varies from flat plateaux to very steep ridges (45°). The altitude of quadrats was usually greater than 1 350 m. The vegetation corresponds closely to Karroid *Merxmuellera* Mountain Veld described by Acocks (1975). Shrub canopy cover is moderate (15%) in quadrats with a mean canopy cover of 71%.

The shrub component consists of evergreen woody shrubs (*Rhus undulata, Buddleja saligna, Euclea crispa* var. *crispa, E. undulata* var. *undulata* and *Olea europaea*) with *Rhus erosa* being a differential species (Figure 9). The leaves of these species are sclerophyllous, dorso-ventrally differentiated and evergreen. These may be an adaptations to the low temperatures and regular snowfalls which occur in the uplands during winter. The inter-clump cover is predominantly grassy, with *Themeda triandra, Cymbopogon plurinodis, Eustachys mutica, Eragrostis* spp., *Merxmuellera disticha* and *Ehrharta calycina* occurring in many of the quadrats. Dwarf shrubs remain a feature, especially *Diospyros austro-africana, Selago bolusii, Rosenia humulis, Pentzia incana, Euryops spathaceus* and *Helichrysum* spp.. The leaves of these species are reduced in size relative to those of the woody shrubs. Succulence is a minor feature of these communities, represented by *Mestoklema* sp., *Crassula* spp., *Othonna cylindrica* and *Lycium* spp..

Grassy Open Shrubland

This variation (community F) is found on both dolerite- and sandstone-dominated slopes and ridges. The dolerite boulders and rocks on the surface are at an advanced stage of oxidization, providing a continual supply of granular, acidic material to the O-horizon. Lidianite is often present immediately adjacent to the dolerite dykes, but as it oxidizes slowly it may not contribute as significantly to soil chemistry. The soils are classed in the Mispah-rock complex, with an orthic A-horizon. The grasses comprise perennial species of the genera *Themeda, Heteropogon, Ehrharta, Cymbopogon, Aristida, Eragrostis, Eustachys, Melica* and *Sporobolus* with canopy cover values varying from 10-100%. Less frequent grass species include *Tetrachne dregeii* and *Helictotrichon turgidulum*.

The grassiness of this variation (Figure 10) may be a consequence of its isolation, and therefore less intensive use by domestic ungulates. The quadrats were located in a relatively inaccessible area where permanent water had only recently been provided, so that these quadrats would represent the more natural condition of the shrubland vegetation. The higher alpha diversity of these quadrats relative to the other quadrats of the Open Shrubland may be an indication of a less disturbed condition.

The geomorphology of this variation is also indicative of the natural condition. There is little evidence of accelerated erosion, and humus-rich topsoil is found both inside and outside woody clumps. The soils are well-drained, with surface moisture penetrating to depths of 50cm and more. The low clay content of the soil means that waterlogging does not occur. The variation contains 5-10% canopy cover of woody shrubs, 40-50% rock and stone cover, and 40-45% Grassy Dwarf Shrubland. Woody shrubs include *Buddleja saligna, Acacia karroo, Grewia robusta, G. occidentalis* and *Rhus* spp.

SUCCULENT THICKET

Quadrats representing this community were usually sampled on concave slopes at altitudes ranging from 800-1 200 m. Soil types range from a Mispah-rock complex to a Mispah-Nyoka-Dudfield Association (Van Riet & Minnaar 1977). Surface rocks were predominantly dolerites, but the underlying parent material was predominantly mudstone. Rocks may account for up to 50% of the cover of a quadrat, and slope is extremely variable. The soils under the clump are minerally poor (Na = 20 ppm, K = 92 ppm) with a low pH (5.8) (Palmer 1988b). Organic content is moderate to low (4.0%) with associated Ca content at 139 ppm.

The differential species in Succulent Thicket on the KNR (community G) include succulent shrubs, deciduous woody shrubs, evergreen shrubs and small trees (Figure 11). *Portulacaria afra* is the most prominent component and one which encouraged Acocks (1975) to call it Succulent Mountain Scrub or Spekboomveld. The *P. afra-Pappea capensis* Association is well defined, with accompanying species including *Carissa haematocarpa, Grewia robusta, Maytenus polyacantha* and *Euclea undulata* (Table 1). Understorey dwarf shrubs and grasses include *Panicum maximum, Abutilon sonneratianum, Peliostomum origanoides* and *Pentzia incana*. The two differential species

Figure 10. The dolerite and sandstone complex of the sloping terrain is covered by Grassy Open Shrubland. Woody shrubs include *Buddleja saligna, Grewia occidentalis, Olea europaea* and *Diospyros austro-africanus.* Characteristic grass species include *Heteropogon contortus, Cymbopogon plurinodis* and *Themeda triandra.*

Figure 11. Succulent Thicket, dominated by *Portulacaria afra*, but containing numerous other woody shrubs of sub-tropical affinity such as *Pappea capensis, Boscia oleoides* and *Carissa haematocarpa.*

Figure 12. Grassy Dwarf Shrublands of the Karoo Nature Reserve, with an indication of the visual contribution which the grass genera *Eragrostis, Aristida, Tragus, Sporobolus* and *Chloris* make to the composition of the landscape.

Figure 13. Situated on the upper pediment, where dolerite boulders are still encountered, Succulent Dwarf Shrubland contains *Senecio longiflorus, Haworthia viscosa* and *Eberlanzia spinosa*.

(*Portulacaria afra* and *Pappea capensis*) occur in 66% of the quadrats, and Van der Walt (1968) reports a similar association from the Noorsveld.

DWARF SHRUBLAND

The formation contains four variations (Figure 6) which reflect the structure of the formation throughout its range. These include Grassy Dwarf Shrubland (H), Succulent Dwarf Shrubland (K), Degraded Dwarf Shrubland (I) and Grassy Dwarf Shrubland of the upper pediment (J). In addition there is a large suite of species which have been described by Werger (1980) as "intruding species" and by Scotcher *et al.* (1978) as "increaser species". I recognized this group of ubiquitous species in the Dwarf Shrublands of the Andries Vosloo Kudu Reserve (Palmer 1981), with representation from the family Compositae, including *Chrysocoma ciliata, Pentzia incana* and *Felicia muricata*. This species group includes dwarf shrubs of medium to low palatability to ungulates, such as *Lycium schizocalyx* and *Protasparagus striatus*, and grasses, including *Aristida congesta* (both subspp.), *Tragus koelerioides, Eragrostis lehmanniana* and *Cynodon incompletus*.

Grassy Dwarf Shrubland

Differential species include *Felicia muricata, Eragrostis obtusa* and *Aristida congesta*. Communities H and I (Figure 12) are distinguishable from one another by the presence of the *Pachypodium succulentum-Blepharis capensis* species group in the former. Infrequent grasses include *Sporobolus nitens, Stipa dregeana, Chloris virgata, Eragrostis bergiana* and *Microchloa caffra*. This grassy condition is found on soils of relatively high pH (7.5 - 8.0), in which the proximity of the $CaCO_3$ layer has probably increased soil alkalinity. Van Riet & Minnaar (1977) describe the soil as a calcareous duplex type of the Nyoka-Mispah Association. The topography is always flat to very gently sloping, with occasional *Acacia karroo* shrubs breaking the landscape. Dwarf shrub height seldom exceeds 1,0 m, and canopy cover varies from 25-50%. Alien species are often present, usually *Salsola kali* and *Atriplex lindleyi (=Blackiella inflata)*. The soil is a sandy loam with relatively high Ca levels (105 ppm).

Succulent Dwarf Shrubland

The landscape in which these communities occur is the flat to very gently sloping pediment, often bisected by drainage patterns of relatively recent origin. The slope angle of the pediment is usually between 0^{o} and 3^{o}, and seldom reaches 7^{o} (Fair 1948). The drainage lines may have developed into pronounced erosion gullies, cutting down four to five metres into the friable alluvium until reaching bedrock.

Soils are generally of the Swartland Form, in which an orthic A-horizon overlies a pedocutanic B-horizon, over saprolite. A layer of silt up to 5cm deep may be deposited over the original soil form. Pedestal formation around the dwarf shrubs is a common feature. The cause of these pedestals needs more investigation, and Norton *et al.* (1985) have provided some techniques for evaluating soil erosion in these pediments.

The moisture and organic content of the soils collected in these communities was very low (2,9 and 2.00 % respectively). Wind appears to be a major factor preventing the accumulation of organic material in the A-horizon. Although no wind data are available for the study area, strong winds are regularly experienced and their role in preventing the accumulation of organic material needs further investigation. The pH of the soils varied from slightly acid (6,7) to alkaline (7,4) (Palmer 1988b). Calcium levels were moderately high (103 ± 5 ppm), but not as high as those in the Grassy Dwarf Shrubland (121 ± 46 ppm). The proportion of sand (< 2 mm fraction only) was high (80.8 ± 6.6 %), giving some justification for the rapid infiltration rates measured (37.5 ml/min.)

Communities J and K are differentiated by four species groups (Table 1). The three succulent species groups are the *Pachypodium succulentum - Blepharis capensis* group, the *Eberlanzia spinosa - Haworthia viscosa* group, and the *Mesembryanthemum karrooense - Psilocaulon articulatum* group. The presence of the latter species group is differential for community K, whereas the other three occur throughout these pediment communities. The relatively high proportion of leaf succulents in each of the groups is an important distinguishing feature (Figure 13). There remain, of course, the dwarf shrub and grass elements in both communities. These elements are common to all communities in the Dwarf Shrubland of the KNR.

Degraded Dwarf Shrubland

The Degraded Dwarf Shrublands are apparently a consequence of recent anthropogenic influences, particularly grazing by sheep (Werger 1980). These communities are the exception rather than the rule on the KNR, and were not specifically sampled in this study of the vegetation and are not represented in Table 1. The vegetation is floristically poor, and the soil surface may display signs of disturbance (ploughing or accelerated erosion). Weedy aliens (e.g. *Atriplex lindleyi and Salsola kali*) and weedy indigenous species (e.g.*Geigeria ornativa* and *Tribulus terrestris*) are present. The ubiquitous species of the *Pentzio-Chrysocomion* (Werger 1980) are usually present, particularly *Pentzia incana, Chrysocoma ciliata, Eragrostis obtusa* and *Felicia muricata. Acacia karroo* and *Cynodon incompletus* are also frequent elements of these communities which are illustrated as Riparian Thicket (Figure 7), reflecting either changes in the water table or inundation owing to the construction of artificial water bodies (Van Rhynevelds Pass Dam). It is essential not to regard these communities as indigenous and a true reflection of the historical nature of the vegetation. The term "transformed natural communities" is preferred, and should be applied in situations where anthropogenic influences are very obvious.

DISCUSSION AND RECOMMENDATIONS

This survey of the vegetation of the KNR has elucidated some aspects of karoo vegetation. These include the nature of the integrated mosaic of formations (Shrubland, Succulent Thicket and Dwarf Shrubland) in the region; the mosaic of floristic units or communities which change over very short distances in the pediments; the gradients in abiotic factors which parallel these floristic changes; and the ability of the vegetation to tolerate extremely intense use from domestic herbivores without undergoing total floristic transformation.

Cowling (1984) suggests the term Subtropical Transitional Thicket to describe the closed large-leaved shrublands which extend from the Tugela River to the south-western Cape, penetrating deep inland when the river valleys provide suitable environments. Communities of similar structure and generic composition are found throughout tropical and sub-tropical Africa (Tinley 1975), and are termed thicket. Acocks (1975) subdivided this thicket into numerous veld types, including Eastern Province Thornveld (southern form), False Thornveld of the Eastern Province, Valley Bushveld (all variations), Noorsveld and Succulent Mountain Veld or Spekboomveld. This list reflects some differences from those suggested by Cowling (1984), and I wish to demonstrate that the flora of the semi-arid study area displays strong affinity with the subtropical flora.

The Subtropical Transitional Thicket contains a succulent element throughout its range, but it is in the south-east that this manifests itself most significantly. Well represented genera include *Portulacaria, Aloe, Crassula, Cotyledon* and *Euphorbia*. It was the presence of these genera in the south-east which prompted Acocks (1975) to describe numerous variations of the Subtropical Transitional Thicket. This was especially noticeable in his treatment of the Valley Bushveld, in which the variations are determined by the presence of a number of endemic Euphorbiaceae, namely *Euphorbia bothae, E. ledienii* and *E. coerulescens*. Earlier analysis of the Spekboomveld suggests a strong affinity between it and other Karoo types (Acocks 1975). The current treatment (Everard 1987) suggests that the affinity is sub-tropical, and I recognized two strong associations which are occur in Valley Bushveld, Noorsveld and Spekbomveld, namely the *Portulacaria afra-Pappea capensis* Association, and the *Euphorbia bothae -Rhigozum obovatum* Association (Palmer 1981). It is the integrity of these associations which lead me to suggest that the Shrublands of the Succulent Transitional Thicket are more closely related to one another than was previously suggested by Acocks (1975), and to expand on the suggested boundaries of Cowling (1984).

Everard (1987) describes in detail the Kaffrarian Succulent Thicket, reporting that it contains both mesic and xeric forms. A comparison between the differential species recognized by Everard (1987) and those of this study, reveals a strong similarity between the Succulent Thicket of the nature reserve and Everard's (1987) Xeric Succulent Thicket. As this formation is structurally distinct from the Dwarf Shrublands and Shrublands of the study area, I suggest the order name Camdebo Xeric Succulent Thicket.

The Succulent Thicket is floristically rich and distinctive and is well preserved on the nature reserve. Anthropogenically-induced change is less apparent in this formation, and management should monitor various elements (seedling recruitment, survival, shrub utilization) of selected woody and succulent species.

Throughout the South African literature, interpretation of pattern in the Dwarf Shrubland has been based largely on the succession theory of Clements (1916). Authors such as Acocks (1975), Tidmarsh (1948, 1952, 1957) and more recently Werger (1980) have suggested that the vegetation is almost exclusively a product of recent human occupation of the region. The current study has not confirmed any of the large-scale transformations of the vegetation which are supposed to have occurred. On the contrary, the Dwarf Shrubland reflects much of the heterogeneity recognized by Marloth (1908).

Small-scale (10 m) mosaics in the vegetation are a feature (Novellie 1987) on small nature reserves in the Nama-Karoo biome. Palmer (1987) reports a similar effect in the Succulent Karoo near Prince Albert, where whistling rats (*Parotomys* sp.) modified the vegetation around their burrows, creating a mosaic of "heuweltjies". It is pertinent in a conservation area to strive for a mosaic of well-preserved and heavily-utilized vegetation. Management on the KNR should aim to achieve patches of Grassy Dwarf Shrubland, Succulent Dwarf Shrubland and Degraded Dwarf Shrubland on the pediments.

The Succulent Dwarf Shrubland at Gannalaagte contains examples of both communities J and K. In the latter case canopy cover is approximately 45%, with leaf succulents accounting for 10% of this cover and other dwarf shrubs only 5%. Weakly perennial and annual grasses account for almost all the balance of cover. This represents a condition which has not been utilized by domestic stock for over 10 years, and does not display a floristic situation very different from the quadrats surveyed earlier (1980) in this study, or from floristically similar situations outside the study area. This raises the questions as to whether recovery rate of vegetation in the karoo is extremely slow, or whether this represents the prevailing climax (Meadows 1985) for the study area. I favour the latter approach in many instances, as the integrity of the floristics appears to have been maintained.

In the Shrublands of the mountainous areas of the eastern and western sections, a policy of patch burning should be applied. The positive effect of this policy is evident in the improved vegetation which developed after an accidental burn near the Valley of Desolation. This policy would reduce the dwarf shrub component which currently predominates between the shrub clumps, and increase grassiness. This policy should be implemented before any further wild ungulates are introduced.

In view of the limited extent and relatively poor quality of the pediments conserved in this nature reserve, it is recommended that further efforts be made to obtain greater areas of the Camdebo plain for addition to this reserve.

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The vegetation of the Karoo Nature Reserve, Cape Province.

II. A preliminary systematic plant species list.

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ABSTRACT

The vegetation of the Karoo Nature Reserve is discussed briefly. The 336 plant species recorded are presented in a checklist. Of the 71 angiosperm families recorded, the Asteraceae (55 spp.), Poaceae (36 spp.), Liliaceae (25 spp.) and Crassulaceae (16 spp.) are those best represented.

UITTREKSEL

Die plantegroei van die Karoo Natuurreservaat word kortliks bespreek. Die 336 plant spesies wat aangeteken is, word weergegee in 'n kontrolelys. Van die 71 angiosperm families wat aangeteken is, is die volgende die beste verteenwoordig: Asteraceae (55 spp.), Poaceae (36 spp.), Liliaceae (25 spp.) en Crassulaceae (16 spp.).

Keywords: checklist, ferns, flowering plants, Karoo

INTRODUCTION

The Karoo Nature Reserve is approximately 16 200 ha in extent, and surrounds the town of Graaff-Reinet, Cape Province. Acocks (1975) recognized four veld types in the study area, namely False Central Lower Karoo, False Karroid Broken Veld, Succulent Mountain Scrub or Spekboomveld, and Karroid *Merxmuellera* Mountain Veld. The vegetation of the study area consists of three distinct physiognomic classes, namely Shrubland, Succulent Thicket and Dwarf Shrubland. The Shrubland is located on the sandstone dominated uplands above 1300 m elevation and displays a gradient from a mesic condition in which the shrubs are separated by grasslands, to a xeric condition in which the inter-clump cover is dominated by dwarf shrubs. The Succulent Thicket is a distinctive unit, dominated by shrubs and succulents of sub-tropical affinity. The Dwarf Shrubland is restricted to the bottomlands, where alkaline alluvial soils are encountered. The Dwarf Shrubland may be grassy, succulent or degraded, depending on the nature of the near-surface substrate, the frequency of precipitation and the recent land-use history.

A study of the vegetation of the reserve was initiated to provide a classification of the vegetation into "ecological units correlated with stable and permanent conditions, distinguishing areas of uniform potential for management purposes" (Coetzee 1974). This included the preparation of this species list and the establishment of a herbarium on the reserve. The species list is a permanent record of the plant species that occurred in the conservation area at the time of its establishment (1976), and serves as a reference collection of the species listed in the phytosociological study. Although this list is incomplete, it provides the basis for the syntaxonomical classification of the vegetation (Palmer 1988).

METHODS

Since its establishment, the Nature Reserve has been visited by various researchers and collectors who have provided material for the compilation of this list. These botanists and nature conservators include O.M. Hilliard, B.L. Burtt, M.T. Linger, C. Newton and R. Allardice. The efforts of these collectors are greatly appreciated, and their contribution to the knowledge of this flora is recorded. In 1980 I initiated a vegetation survey of the reserve using the Braun-Blanquet phytosociological technique. Voucher specimens collected during this survey are deposited in the Karoo Nature Reserve Herbarium (1st collection), PRE (1 st duplicate) and GRA (2nd duplicate).

The Pteridophyta are arranged according to the classification system of Schelpe (1969), while the Angiospermae are arranged in families and genera according to Dyer (1975, 1976), as based upon De Dalla Torre & Harms (1958). In the case of the Poaceae, the genus numbers appearing in the text are based on the Hubbard system, whereas the genus numbers within all other families are based upon De Dalla Torre & Harms (Dyer 1975, 1976). Author names are in agreement with Gibbs Russell *et al.* (1985, 1987).

In order to assess possible additions to the list, the PRECIS listings (Gibbs Russell 1985) for the quarter degree squares 3224 AB, AD, BA and BC were examined for similarity. All common species were noted and the possible additional species estimated. The naturalised aliens are listed according to MacDonald (1983), Wells *et al.* (1986) and Gibbs Russell *et al.* (1987) and have been included.

RESULTS AND DISCUSSION

A total of 327 indigenous plant species were collected in the study area, together with nine naturalised aliens. These species represent 191 genera and 71 families (Table 1). Analysis of the species list reveals that nine families account for 190 species, or 56,2% of all species.

Possible additional species amount to 223 (Table 2). A review of the recent revision of the genus *Helichrysum* (Hilliard 1983) yielded 16 possible additional species for the study area. These additional species are not included in the list (Table 3).

With cryptogams and naturalised aliens being seriously under-collected, I estimate that this list represents 40 - 50 % of the flora of the reserve. It is essential to view this checklist within these constraints. The flora of the region has been historically under-collected and new efforts should be initiated to remedy this situation throughout the karoo biome. The number of specimens recorded from the reserve, but not listed in PRECIS (43,5%), is indicative of the representativeness of the PRECIS database and for this area. This study provides support for an effort to intensify collecting in this region.

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Table 1. The number of genera and species in the plant families on the Karoo Nature Reserve.

Family	Genera	Species
Pteridophyta		
Adiantaceae	1	2
Angiospermae		
Poaceae	25	36
Cyperaceae	2	3
Commelinaceae	1	1
Juncaceae	1	1
Liliaceae	10	25
Amaryllidaceae	2	2
Dioscoreaceae	1	1
Iridaceae	2	2
Salicaceae	1	1
Ulmaceae	1	1
Moraceae	1	1
Urticaceae	1	1
Loranthaceae	1	1
Viscaceae	1	1
Santalaceae	2	6
Polygonaceae	1	1
Chenopodiaceae	3	5
Nyctaginaceae	1	1
Aizoaceae	4	4
Mesembryanthemaceae	9	10
Portulacaceae	1	1
Caryophyllaceae	1	1
Illecebraceae	2	2
Ranunculaceae	1	1
Menispermaceae	1	1
Brassicaceae	2	3
Capparaceae	2	2
Crassulaceae	4	16
Fabaceae		
Mimosoideae	1	1
Caesalpinioideae	1	1
Papilionoideae	6	11
Geraniaceae	2	10
Oxalidaceae	1	2

Zygophyllaceae	2	4
Rutaceae	1	1
Polygalaceae	1	3
Euphorbiaceae	2	4
Anacardiaceae	1	9
Celastraceae	1	4
Sapindaceae	2	2
Rhamnaceae	1	1
Vitaceae	1	2
Tiliaceae	1	2
Malvaceae	5	5
Sterculiaceae	1	14
Tamaricaceae	1	1
Flacourtiaceae	1	1
Thymelaeaceae	1	1
Araliaceae	1	2
Myrsinaceae	1	1
Ebenaceae	2	7
Oleaceae	1	1
Loganiaceae	1	2
Apocynaceae	2	2
Asclepiadaceae	3	5
Convolvulaceae	1	1
Boraginaceae	1	1
Verbenaceae	3	3
Lamiaceae	4	4
Solanaceae	2	6
Scrophulariaceae (A)	7	13
Selaginaceae	2	5
Scrophulariaceae (B)	1	1
Bignoniaceae	1	1
Gesneriaceae	1	1
Acanthaceae	4	7
Rubiaceae	1	1
Dipsacaceae	1	1
Cucurbitaceae	2	2
Campanulaceae	1	1
Lobeliaceae	1	1
Asteraceae	29	55
Total	191	336

Table 2. A comparison of the species list of the plants of the Karoo Nature Reserve with other sources of taxon lists for the area.

Quarter degree square	No. of species common to PRECIS	No. of additional species	No. of species only on this list	Possible Hilliard (1983) additions	Possible total number
3224 BC	135	194	203	16	
3224 BA, AB, DA	20	27			
					575

Table 3. A preliminary systematic plant species list of the Karoo Nature Reserve.

* = alien to southern Africa.
Collectors' codes: A = R. Allardice; L = M.T. Linger; N = C. Newton; H&B = O.M. Hilliard and B.L. Burtt; P = A.R. Palmer

	PTERIDOPHYTA	
Adiantaceae		
	Cheilanthes Swartz	
	C. hirta Swartz	A 1504
	C. marlothii (Hieron.) Schelpe	L 2041
	ANGIOSPERMAE-MONOCOTYLEDONAE	
Poaceae		
K72	*Cymbopogon* Spreng.	
	C.marginatus (Steud.) Stapf ex Burtt Davy	P 700
	C. plurinodis (Stapf) Stapf ex Burtt Davy	A 1589
K73	*Hyparrhenia* Anderss. ex Fourn.	
	H. hirta (L.) Stapf	A 1502
K80	*Heteropogon* Pers.	
	H. contortus (L.) Roem. & Schult.	P 527, A 1586
K83	*Themeda* Forssk.	
	T. triandra Forssk.	N 2
K89	*Digitaria* Haller	
	D. eriantha Steud.	A 1509, 1617, P 529
K116	*Panicum* L.	
	P. maximum Jacq.	A 1580, 1613
K128	*Setaria* Beauv.	
	S. sphacelata (Schumach.) Moss	
	var. *sphacelata*	P 1064
K132a	*Rhynchelytrum* Nees	
	R. repens (Willd.) C.E. Hubb.	A 1594
K140	*Cenchrus* L.	
	C. ciliaris L.	A 1590, P 1025
K160	*Ehrharta* Thunb.	
	E. calycina J.E. Sm.	
	var. *angustifolia* Kunth	A 1508, 1582
K204c	*Merxmuellera* Conert	
	M. disticha (Nees) Conert	P 859
K214	*Phragmites* Trin.	
	P. australis (Cav.) Steud.	P 948
K260a	*Stipagrostis* Nees	
	S. obtusa (Del.) Nees	A 1575
K262	*Aristida* L.	
	A. adscensionis L. subsp.	
	guineensis (Trin. & Rupr.) Henr.	A 1577
	A. congesta Roem. & Schult. subsp.	
	barbicollis (Trin. & Rupr.) de Winter	P 736

	A. congesta Roem. & Schult.	
	subsp. *congesta*	P 748
	A. diffusa Trin.	
	var. *burkei* (Stapf) Meld.	P 535
K263	*Stipa* L.	
	S. dregeana Steud.	
	var. *elongata* (Nees) Stapf	L 2063
K274	*Tragus* Haller	
	T. berteronianus Schult.	A 1619
	T. koeleroides Aschers.	A 1592
	T. racemosus (L.) All.	A 864
K283	*Sporobolus* R. Br.	
	S. fimbriatus (Trin.) Nees	
	var. *fimbriatus*	P 577
	S. nitens Stent	P 1060
K286	*Eragrostis* Beauv.	
	E. curvula (Schrad.) Nees	P 543, 619
	E. lehmanniana Nees var. *lehmanniana*	P 1260
	E. obtusa Munro ex Fical. & Hiern	P 501, A 1618
	E. sp.	A 1581
K296	*Cynodon* Rich. ex Pers.	
	C. dactylon (L.) Pers.	P 467
	C. incompletus Nees	A 1608
K301	*Chloris* Swartz	
	C. virgata Swartz	P 550
K302	*Eustachys* Desv.	
	E. paspaloides (Vahl) Lanza & Mattei	P 904
K357	*Enneapogon* Desv. ex Beauv.	
	E. scoparius Stapf	P 874
K371	*Fingerhuthia* Nees	
	F. sesleriiformis Nees	P 564
K386	*Melica* L.	
	M. racemosa Thunb.	P 517
K428	*Bromus* L.	
	**B. unioloides* H.B.K.	A 1604
Cyperaceae		
459c	*Mariscus* Gaertn.	
	M. rehmannianus C.B. Cl.	A 1620
	M. vestitus (Hochst. ex Krauss) C.B. Cl.	A 1620
465	*Ficinia* Schrad.	
	F. trichodes (Schrad.)Benth. & Hook. f.	P 695
Commelinaceae		
896	*Commelina* L.	
	C. africana L. var. *barberae* C.B. Cl.	P 587, N (sn)
Juncaceae		
936	*Juncus* L.	
	J. effusus L.	P 583
Liliaceae		
969	*Androcymbium* Willd.	
	A. melanthioides Willd.	N (sn)

985	*Bulbine* Willd.	
	B. abyssinica A. Rich.	L 2013, P 574
	B. frutescens (L.) Willd.	L 2016
	B. narcissifolia Salm-Dyck	L 2021
	B. sp.	H&B 10733
1010	*Schizobasis* Bak.	
	S. intricata (Bak.) Bak.	A 1591
1026	*Aloe* L.	
	A. ferox Mill.	L 2147
	A. longistyla Bak.	L 2104
	A. microstigma Salm-Dyck	L 2119
	A. striata Haw.	L 2143, 2113
	A. variegata L.	L 2149
1029	*Haworthia* Duval	
	H. arachnoidea (L.) Duval	L 2133
	H. viscosa (L.) Haw.	L 2128
1084	*Dipcadi* Medic.	
	D. viride (L.) Moench	P 705
1085	*Litanthus* Harv.	
	L. pusillus Harv.	H&B 10749
1098	*Lachenalia* Jacq. f. ex Murray	
	L. bowkeri Bak.	L 2099
1110	*Sansevieria* Thunb.	
	S. aethiopica Thunb.	A 1585
1113	*Protasparagus* L.	
	P. acocksii Jessop	A 1544
	P. laricinus Burch.	L 2026
	P. racemosus Willd.	P 605, L2117
	P. retrofractus L.	L 2029
	P. setaceus (Kunth) Jessop	L 2072
	P striatus (L. f.) Thunb.	P 496, L 2059
	P. suaveolens (Burch.) Oberm.	A 1540, P 593, L 2028
	P. subulatus Thunb.	P 483, A 1591
Amaryllidaceae		
1167	*Haemanthus* L.	
	H. albiflos Jacq.	L 2136
1168	*Boophane* Herb.	
	B. disticha (L. f.) Herb.	P 749
Dioscoreaceae		
1252	*Dioscorea* L.	
	D. elephantipes (L'Hérit.) Engl.	P 513
Iridaceae		
1265	*Moraea* Mill.	
	M. polystachya (Thunb.) Ker-Gawl.	L 2022, 2098
1301	*Hesperantha* Ker-Gawl.	
	H. longituba (Klatt) Bak.	L 2106

ANGIOSPERMAE - DICOTYLEDONAE

Salicaceae		
1873	*Salix* L.	
	S. mucronata Thunb. var. *mucronata*	P (sn)
Ulmaceae		
1898	*Celtis* L.	
	C. africana Burm. f.	P 937
Moraceae		
1961	*Ficus* L.	
	F. burtt-davyi Hutch.	A 1610
Urticaceae		
2012	*Forsskaolea* L.	
	F. candida L. f. var. *candida*	L 2070
Loranthaceae		
2074	*Moquinella* Balle	
	M. rubra (Spreng. f.) Balle	L 2043
Viscaceae		
2093	*Viscum* L.	
	V. obscurum Thunb.	P 511
Santalaceae		
2108	*Osyris* L.	
	O. lanceolata Hochst. & Steud.	H&B 10737
2118	*Thesium* L.	
	T. imbricatum Thunb.	A 1567
	T. lineatum L. f.	L 2082
	T. namaquense Schltr.	P 609
	T. scandens Sond.	L 2146
	T. sp.	P 556
Polygonaceae		
2194	*Emex* Neck. ex Campd.	
	E. australis Steinh.	L 2097
Chenopodiaceae		
2223	*Chenopodium* L.	
	C. phillipsianum Aell.	A 1547
	**C. schraderanum* Roem. & Schult.	L 2010
2229a	**Atriplex* L.	
	A. lindleyi Moq. subsp. *inflata* (Muell.) P.G. Wilson	A 1550, P 454
2269	*Salsola* L.	
	S. aphylla L. f.	P 472
	**S. kali* L.	A 1598
Nyctaginaceae		
2349	*Boerhavia* L.	
	**B. cordobensis* Kuntze	P 460
Aizoaceae		
2390	*Hypertelis* E. Mey. ex Fenzl	
	H. bowkeriana Sond.	P 1102
2395	*Trianthema* L.	
	T. triquetra Willd. subsp. *parvifolia* (Sond.)Jeffrey	A 1607

2399	*Galenia* L.	
	G. sarcophylla Fenzl	L 2033
2401	*Aizoon* L.	
	A. rigidum L. f. var. *angustifolium*Sond.	A 1519
Mesembryanthemaceae		
2405	*Delosperma* N.E. Br.	
	D. lehmannii (Eckl. & Zeyh.) Schwant.	P 572
	D. sp.	L 2056
2405	*Eberlanzia* Schwant.	
	E. spinosa (L.) Schwant.	L 2132, P 548
2405	*Glottiphyllum* N.E. Br.	
	G. sp.	L 2112
2405	*Malephora* N.E. Br.	
	M. sp.	L 2032, 2127
2405	*Mesembryanthemum* L.	
	M. karrooense L. Bol.	L 2140
2405	*Mestoklema* N.E.Br.	
	M. tuberosum (L.) N.E. Br. ex Glen var. *tuberosum*	L 2052, 2018, P 607
2405	*Pleiospilos* N.E. Br.	
	P. bolusii (Hook.f.)N.E. Br.	A 1609
2405	*Psilocaulon* N.E. Br.	
	P. articulatum (Thunb.) Schwant.	L 2046,2142,2144
2405	*Trichodiadema Schwant.*	
	T. sp.	L 2051
Portulacaceae		
2419	*Portulacaria* L.	
	P. afra Jacq.	A 1579
Caryophyllaceae (Part A)		
2429	**Stellaria* L.	
	S. media (L.) Vill.	L 2125
Illecebraceae		
2467	*Pollichia* Ait.	
	P. campestris Ait.	L 2094
2502	*Dianthus* L.	
	D. namaensis Schinz var. *namaensis*	H&B 10717
Ranunculaceae		
2542	*Clematis* L.	
	C. brachiata Thunb.	A 1572
Menispermaceae		
2573	*Antizoma* Miers	
	A. capensis L. f.	A 1503
Brassicaceae		
2875	*Heliophila* L.	
	H. carnosa (Thunb.) Steud.	A 1562
	H. minima (Stephens) Marais	L 2068
2883	*Lepidium* L.	
	L. africanum (Burm.f.)DC.subsp. *divaricatum* (Ait.) Jonsell	P 243

Capparaceae		
3106	*Boscia* Lam.	
	B. oleoides (Burch. ex DC.) Toelken	L 2088, P 825
3109	*Cadaba* Forssk.	
	C. aphylla (Thunb.) Wild	A 1, P 1069
Crassulaceae		
3164	*Cotyledon* L.	
	C. orbiculata L. var. *orbiculata*	L 2129, 2130
	C. sp.	H&B 10734
3166	*Kalanchoe* Adans.	
	K. rotundifolia (Haw.) Haw.	L 2080
3168	*Crassula* L.	
	C. capitella Thunb.	
	subsp. *thyrsiflora* Toelken	P 615, A 1593
	C. corallina Thunb.	
	subsp. *corallina*	A 1557
	C. expansa Dryand. subsp. *expansa*	A 1511
	C. muscosa L. var. *muscosa*	A 1527, A 1588
	C. nemorosa (Eckl. & Zeyh.)	
	Endl. ex Walp.	L 2083
	C. ovata (Mill.) Druce	A 1532
	C. pubescens Thunb. subsp. *pubescens*	H&B 10744
	C. rogersii Schonl.	P 491
	C. rupestris Thunb. subsp. *rupestris*	L 2081, P 559
	C. sarcocaulis Eckl. & Zeyh.	
	subsp. *sarcocaulis*	A 1595
	C. tetragona L. subsp. *tetragona*	P 617
3175	*Adromischus* Lem.	
	A. cooperi (Bak.) Berger	H&B 10750
	A. triflorus (L. f.) Berger	A 1587
Fabaceae		
Mimosoideae		
3446	*Acacia* Mill.	
	A. karroo Hayne	A 1576
Caesalpinioideae		
3506	*Schotia* Jacq.	
	S. afra (L.) Thunb. var. *afra*	P 633
Papilionoideae		
3657	*Lotononis* (DC.) Eckl. & Zeyh.	
	L. sp. cf. *L. depressa* Eckl. & Zeyh.	A 1616
3665	*Melolobium* Eckl. & Zeyh.	
	M. candicans (E. Mey.) Eckl. & Zeyh.	L 2107, P 876
3673	*Argyrolobium* Eckl. & Zeyh.	
	A. barbatum Walp.	L 2095
	A. variopile N.E. Br.	L 2091
3702	*Indigofera* L.	
	I. argyraea Eckl. & Zeyh.	L 2015, 2096
	I. heterophylla Thunb.	P 503, 542
	I. sp. cf. *I. denudata* Thunb.	P 589
3754	*Sutherlandia* R.Br. ex Ait.f.	
	S. humilis Phill. & R.A.Dyer	L 2053

3756	*Lessertia* DC.	
	L. annularis Burch.	L 2093
	L. depressa Harv.	A 1538, L 2049
	L. physodes Eckl. & Zeyh.	L 2053
Geraniaceae		
3926	*Sarcocaulon* (DC.) Sweet	
	S. camdeboense Moffett	L 2001, P 534
	S. vanderietiae L. Bol.	L 2134
3928	*Pelargonium* L'Hérit.	
	P. abrotonifolium (L. f.) Jacq.	A 1506, P 614
	P. aridum R.A. Dyer	A 1614
	P. carnosum (L.) L'Hérit.	A 1615
	P. trifidum Jacq.	A 1584
	P. glutinosum (Jacq.) L'Hérit.	H&B 10711
	P. myrrhifolium (L.)L'Hérit. var. *myrrhifolium*	P 613, A 1596
	P. zonale (L.) L'Hérit.	H&B 10710, A1611
	P. sp.	A 1614
Oxalidaceae		
3936	*Oxalis* L.	
	O. bowiei Lindl.	A 1531
	O. pes-caprae L. var. *pes-caprae*	L 2079
Zygophyllaceae		
3965	*Zygophyllum* L.	
	Z. gilfillani N.E. Br.	A 1541, L 2057
	Z. microcarpum Licht. ex Cham. & Schlechtd.	A 1553, L 2109
	Z. retrofractum Thunb.	A 1552, L 2034
3978	*Tribulus* L.	
	T. terrestris L.	P 630, A 1617
Rutaceae		
4076	*Vepris* Comm. ex A. Juss.	
	V. undulata (Thunb.) Verdoorn & C.A. Sm.	P 620
Polygalaceae		
4273	*Polygala* L.	
	P. asbestina Burch.	P 514
	P. ephedroides Burch.	A 1526, L 2017
	P. hottentotta Presl	P 594
Euphorbiaceae		
4299	*Phyllanthus* L.	
	P. sp.	H&B 10736
4498	*Euphorbia* L.	
	E. mauritanica L. var. *mauritanica*	P 560, L 2050
	E. sp. cf. *E. ferox* Marloth	L 2135
	E. sp.	L 2077

Anacardiaceae		
4594	*Rhus* L.	
	R. erosa Thunb.	A 1539
	R. incisa L. f. var. *incisa*	A 1554, 1583, P 1023
	R. lancea L. f.	A 787
	R. pentheri Zahlbr.	A 1533
	R. refracta Eckl. & Zeyh.	L 2137, P 477
	R. rigida Mill.	A 1573
	R. undulata Jacq.	A 1516
	R. longispina Eckl. & Zeyh.	L 2090
	R. sp.	P 691
Celastraceae		
4626	*Maytenus* Molina	
	M. capitata (E. Mey. ex Sond.) Marais	L 2103
	M. heterophylla (Eckl.& Zeyh.) N.K.B.Robson	P 484
	M. linearis (L. f.) Marais	P 567, L 2061
	M. polyacantha (Sond.) Marais	L 2139
Sapindaceae		
4784	*Pappea* Eckl. & Zeyh.	
	P. capensis Eckl. & Zeyh.	P 474, L 2121
4831	*Dodonaea* Mill.	
	D. angustifolia L. f.	A 1571
Rhamnaceae		
4875	*Rhamnus* L.	
	R. prinoides L'Hérit.	A 1554
Vitaceae		
4917	*Rhoicissus* Planch.	
	R. rhomboidea (E. Mey. ex Harv.) Planch.	L 2120
	R. tridentata (L. f.) Wild & Drum.	P 495, 476
Tiliaceae		
4966	*Grewia* L.	
	G. occidentalis L.	P 525, L 2024
	G. robusta Burch.	P 473.
Malvaceae		
4983	*Abutilon* Mill.	
	A. sonneratianum (Cav.) Sweet	L 2012, P 629
4986a	*Anisodontea* Presl	
	A. malvastroides (Bak. f.) Bates	H&B 10708, A 1570
4998	*Sida* L.	
	S. ternata L. f.	L 2123
5013	*Hibiscus* L.	
	H. pusillus Thunb.	L 2011, 2002, P 523
5013a	*Radyera* Bullock	
	R. urens (L. f.) Bullock	L 2105

Sterculiaceae		
5056	*Hermannia* L.	
	H. bryoniifolia Burch.	L 2074
	H. cernua Thunb.	A 1565, L 2148
	H. cuneifolia Jacq. var. *cuneifolia*	L 2138
	H. cuneifolia Jacq. var. *glabrescens*	A 1543
	H. erodioides (Burch. ex DC.) Kuntze	H&B 10726
	H. filifolia L. f. var. *filifolia*	L 2037, H&B 10725
	H. glabrata L. f.	L 2071
	H. gracilis Eckl. & Zeyh.	A 1530
	H. holosericea Jacq.	L 2062
	H. pulverata Andr.	A 1555, 1558
	H. sulcata Harv.	P 627
	H. vestita Thunb.	H&B 10730
	H. sp. cf. *H. muricata* Eckl. & Zeyh.	A 1535, H&B 10728
	H. sp. cf. *H. coccocarpa* (Eckl. & Zeyh.) Kuntze	H&B 10726
Tamaricaceae		
5239	**Tamarix* L.	
	T. usneoides E. Mey. ex Bunge	A 1599
Flacourtiaceae		
5296	*Kiggelaria* L.	
	K. africana L.	L 2044
Thymelaeaceae		
5435	*Gnidia* L.	
	G. microphylla Meisn.	L 2014
Araliaceae		
5872	*Cussonia* Thunb.	
	C. paniculata Eckl. & Zeyh.	L 2047, 2054
	C. spicata Thunb.	A 1514, 1522
Myrsinaceae		
6313	*Myrsine* L.	
	M. africana L.	P 696
Ebenaceae		
6404	*Euclea* Murray	
	E. crispa (Thunb.) Guerke subsp. *crispa*	P 1061
	E. undulata Thunb. var. *undulata*	A 1525, P 482
6406	*Diospyros* L.	
	D. austro-africana De Winter	P 554
	D. lycioides Desf. subsp. *lycioides*	L 2141
	D. ramulosa (E. Mey. ex A. DC.) De Winter	L 2086
	D. villosa (L.) De Winter var. *villosa*	P 539
	D. sp.	P 705
Oleaceae		
6434	*Olea* L.	
	O. europaea L. subsp. *africana* (Mill.) P.S.Green	A 1551

Loganiaceae		
6473	*Buddleja* L.	
	B. glomerata Wendl. f.	A 1521, H&B 10746
	B. saligna Willd.	A 1524, H&B 10729
Apocynaceae		
6559	*Carissa* L.	
	C. haematocarpa (Eckl.) A. DC.	P 475
6681	*Pachypodium* Lindl.	
	P. succulentum (L. f.) Sweet	H&B 10732
Asclepiadaceae		
6791	*Asclepias* L.	
	A. burchellii Schltr.	L 2019, A 1621
	A. cancellata Burm. f.	P 698
	A. fruticosa L.	A 1621
6849	*Sarcostemma* R.Br.	
	S. viminale (L.) R.Br.	P383
6885	*Tridentea* Haw.	
	T. sp. cf. *T. gemmiflora* (Mass.) Haw.	A 1523
Convolvulaceae		
6993	*Convolvulus* L.	
	C. sagittatus Thunb.var.*ulosepalus* (Hallier f.) Verdc.	P 468
Boraginaceae		
7043	*Ehretia* P.Br.	
	E. rigida (Thunb.) Druce	P 565, 624
Verbenaceae		
7144	*Lantana* L.	
	L. rugosa Thunb.	L 2008, P 557
7145a	*Phyla* Lour.	
	P. nodiflora (L.) Greene var. *nodiflora*	L 2048, A 1606
7148	*Plexipus* Rafin.	
	P. cuneifolius (L. f.) Rafin.	P 1062
Lamiaceae		
7212	*Teucrium* L.	
	T. africanum Thunb.	A 1534
7281	*Stachys* L.	
	S. scabrida Skan	A 1501
7290	*Salvia* L.	
	S. repens Burch. ex Benth. var. *repens*	P 1060
7366a	*Becium* Lindl.	
	B. burchellianum (Benth.) N.E. Br.	A 1529, H&B 10747
Solanaceae		
7379	*Lycium* L.	
	L. cinereum Thunb.	P 545
	L. oxycarpum Dun.	A 1520, L 2003
	L. schizocalyx C.H. Wr.	L 2030
	L. sp.	P 573
7407	*Solanum* L.	
	S. coccineum Jacq.	P 516
	**S. elaeagnifolium* Cav.	N 1

Scrophulariaceae (Part A)		
7467	*Aptosimum* Burch.	
	A. procumbens (Lehm.)Steud. var. *procumbens*	L 2004
7468	*Peliostomum* Benth.	
	P. origanoides E. Mey. ex Benth.	P 510
7471	*Diascia* Link & Otto	
	D. capsularis Benth.	L 2023
7476	*Nemesia* Vent.	
	N. fruticans (Thunb.) Benth.	L 2076
	N. hanoverica Hiern	L 2055
7519	*Sutera* Roth	
	S. albiflora Verdoorn	L 2042
	S. caerulea (L. f.) Hiern	A 1622
	S. halimifolia (Benth.) Kuntze	H&B 10712
	S. mollis (Benth.) Hiern	L 2006, H&B 10727
	S. pinnatifida (Benth.) Kuntze	P 498
7522	*Polycarena* Benth.	
	P. capillaris (L. f.) Benth.	A 1548
7523	*Zaluzianskya* F.W. Schmidt	
	Z. africana (Thunb.) Hiern	A 2561
	Z. crocea Schltr.	L 2064
Selaginaceae		
7568	*Selago* L.	
	S. albida Choisy	P 880, P 1022
	S. bolusii Rolfe	H&B 10735
	S. corymbosa L.	P 621
7568a	*Walafrida* E. Mey.	
	W. geniculata (L. f.) Rolfe	L 2005, P 492
	W. saxatilis (E. Mey.) Rolfe	A 1518, 1615
Scrophulariaceae (Part B)		
7597a	*Alectra* Thunb.	
	A. pumila Benth.	A 1546
Bignoniaceae		
7722	*Rhigozum* Burch.	
	R. obovatum Burch.	P 968
Gesneriaceae		
7823	*Streptocarpus* Lindl.	
	S. meyeri B.L. Burtt	H&B 10724
Acanthaceae		
7973	*Barleria* L.	
	B. irritans Nees	P 504
	B. obtusa Nees	A 1624
7980	*Blepharis* Juss.	
	B. capensis (L. f.) Pers. var. *capensis*	H&B 10719
	B. villosa (Nees) C.B. Cl.	H&B 10715, L 2084
8094	*Justicia* L.	
	J. cuneata Vahl subsp. *cuneata*	P 561
	J. sp.	P 595
8094a	*Monechma* Hochst.	
	M. spartioides (T.Anders)C.B. Cl.	A 1542, L 2067

Rubiaceae		
8486	*Galium* L.	
	G. tomentosum Thunb.	L 2025
Dipsacaceae		
8546	*Scabiosa* L.	
	S. columbaria L.	H&B 10731
Cucurbitaceae		
8568	*Kedrostis* Medik.	
	K. africana (L.) Cogn.	P 566
8599	*Cucumis* L.	
	C. myriocarpus Naud. subsp. *leptodermis* (Schweick.) C. Jeffrey & P. Halliday	L 2101
Campanulaceae		
8670	*Lightfootia* L'Hérit.	
	L. albens Spreng. ex A. DC.	A 1597
Lobeliaceae		
8681	*Cyphia* Berg.	
	C. sylvatica Eckl. var. *sylvatica*	P 905
Asteraceae		
8862	*Pteronia* L.	
	P. adenocarpa Harv.	A 1568
	P. glauca Thunb.	A 1510
8887	*Amellus* L.	
	A. strigosus (Thunb.) Less. subsp. *strigosus*	H&B 10722
	A. strigosus (Thunb.) Less. subsp. *pseudoscabrinus* Rommel	L 2102
8919	*Felicia* Cass.	
	F. filifolia (Vent.) Burtt Davy subsp. *filifolia*	A 1512,P 555
	F. hirsuta DC.	P 461
	F. hyssopifolia (Berg.) Nees subsp. *polyphylla* (Harv.)Grau	L 2009, P 590
	F. muricata (Thunb.) Nees subsp. *muricata*	P 549
	F. ovata (Thunb.) Compton	L 2066, P 879
8930	*Chrysocoma* L.	
	C. ciliata L.	A 1560
8992	*Gnaphalium* L.	
	G. capense Hilliard	H&B 10740
	G. confine Harv.	H&B 10743
8992a	*Pseudognaphalium* Kirp.	
	P. luteo-album (L.) Hilliard & Burtt	A 1605
8992b	*Troglophyton* Hilliard & Burtt	
	T. capillaceum (Thunb.) Hilliard & Burtt subsp. *capillaceum*	L 2075

9006	*Helichrysum* Mill.	
	H. cymosum (L.) D. Don subsp. *cymosum*	A 1536
	H. hamulosum E. Mey. ex DC.	P 531
	H. pumilio (O.Hoffm.) Hilliard & Burtt subsp. *pumilio*	A 1505
	H. rosum (Berg.) Less. var. *rosum*	P 520
9041	*Elytropappus* Cass.	
	E. rhinocerotis (L. f.) Less.	P 530
9050	*Rosenia* Thunb.	
	R. humilis (Less.) Bremer	A 1513, P 547, L 211
9073	*Pegolettia* Cass.	
	P. baccharidifolia Less.	A 1507, 1566
	P. retrofracta (Thunb.) Kies	P 591
9090	*Geigeria* Griesselich	
	G. ornativa O. Hoffm.	L 2031
9306	*Gaillardia* Foug.	
	**G. pulchella* Foug.	A 1600
9320	*Eriocephalus* L.	
	E. africanus L.	P 1011
	E. ericoides (L. f.) Druce	A 1517, P 521
9336	*Phymaspermum* Less. emend. Kallersjo	
	P. parvifolium (DC.) Benth. & Hook.	L 2126
9351	*Cotula* L.	
	C. anthemoides L.	H&B 10721
	C. sororia DC.	H&B 10738
9366	*Pentzia* Thunb.	
	P. incana (Thunb.) Kuntze	A 1537
	P. pilulifera (L. f.) Fourc.	L 2115
	P. punctata Harv.	P 690
9406	*Cineraria* L.	
	C. alchemilloides DC.	L 2065
	C. aspera Thunb.	L 2058
	C. mollis E. Mey. ex DC.	H&B 10742
	C. sp.	H&B 10741
9411	*Senecio* L.	
	S. acutifolius DC.	P 1528
	S. angustifolius (Thunb.) Willd.	L 2114
	S. cotyledonis DC.	L 2100
	S. junceus (DC.) Harv.	A 1569
	S. laevigatus Thunb. var. *laevigatus*	A 1528, P 586
	S. longiflorus (DC.) Sch. Bip.	A 1556, P 458
	S. radicans (L. f.) Sch. Bip.	L 2131, P 1056
9417	*Euryops* Cass.	
	E. anthemoides B. Nord. subsp. *astrotrichus* B. Nord.	P 512
	E. spathaceus DC.	L 2020, P 515
9420	*Othonna* L.	
	O. cylindrica (Lam.) DC.	L 2085, P 600
9425	*Dimorphotheca* Vaill. ex Moench	
	D. zeyheri Sond.	A 1513, L 2007

9427	*Osteospermum* L.	
	O. calendulaceum L. f.	L 2073, 2111
	O. scariosum DC. var. *scariosum*	L 2092, P 1017
9431	*Ursinia* Gaertn.	
	U. nana DC. subsp. *nana*	A 1549
9432	*Arctotis* L.	
	A. sulcocarpa Lewin	L 2035
9438	*Berkheya* Ehrh.	
	B. cardopatifolia (DC.) Roessl.	P 687
9438a	*Cuspidia* Gaertn.	
	C. cernua (L. f.) B.L.Burtt subsp. *annua* (Less.)Roessl.	L 2069
9462	**Cirsium* Mill.	
	C. vulgare (Savi) Ten.	A 1601
9501	*Dicoma* Cass.	
	D. spinosa (L.) Druce	A 1545, P 536

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Plant/soil relationships in the central area of the Cape midlands, South Africa.

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ABSTRACT

Surface soil samples of the Shrublands, Succulent Thicket and Dwarf Shrublands of the Camdebo and Sneeuberg regions were collected. Each sample was analysed for field moisture content, organic matter content, pH, conductivity, Ca, Mg, K, Na, P and texture. The results were subjected to ordination by means of principal component analysis and compared with a structural/floristic classification of the vegetation arrived at using the methods of the Zürich-Montpellier approach. The ordination identified a gradient of decreasing Ca, Mg and conductivity values from the minerally rich sites of the Shrubland and the Grassy Dwarf Shrubland to the leached conditions of the mesic Grasslands. Another gradient of increasing Na levels and concomitant increase in silt and pH, paralleled the gradient from mesic Grasslands of the mountains to Succulent and Grassy Dwarf Shrublands of the pediments.

UITTREKSEL

Die gronde van die Struikveld, Sukkulente Bosveld en Dwerg Struikveldveld van die Camdebo en Sneeuberg streke is gemonster. Elke monster is vir water inhoud, organiese-inhoud, pH, konduktiwiteit, Ca, Mg, K, Na, P en korrelgrootteverspreiding ge-analiseer. Die resultate is deur middel van hoof komponente analise ge-orden en hierdie resultaat is vergelyk met die strukturele-floristiese klassifikasie van die plantegroei wat is met behulp van die Zürich-Montpellier fitososiologiese benadering en metodiek bepaal is. Die ordening het 'n gradient van vermindering in Ca, Mg en konduktiwiteit van die mineraal-ryk Struikveld en die Grasagtige Dwerg Struikveld tot die uitgeloogde mesiese Grasveld uitgewys. 'n Verdere gradient van toename in Na, slik en pH, loop met die gradient van die nat Grasveld van die berge tot Sukkulente en Grasagtige Dwerg Struikveld.

Keywords: Karoo, soil, vegetation.

INTRODUCTION

In the interpretation of environmental gradients responsible for differentiating plant communities, Palmer *et al.* (1988) used principal component analysis of surface soil characteristics. This type of multivariate analysis assists in elucidating the environmental gradients operating in natural ecosystems (Gower, 1969; Whittaker, 1975; Kessell, 1979; Webster, 1979). The selection of variables to measure and subject to multivariate analysis is, however, a much more important decision and it is necessary to establish an hypothesis before attempting to collect environmental data. In this study, total floristic information was collected at selected sites in the Camdebo and Sneeuberg region of the Nama-Karoo Biome (Palmer, 1988) and used to develop a syntaxonomic classification of the vegetation. It was decided to test the integrity of the classification by measuring soil variables at points along the indirect vegetation gradient. This is in accordance with the suggestion of Kessell (1979) that if a phytosociological classification achieved by indirect gradient analysis corresponds to an environmental gradient, the methods of direct gradient analysis may be employed to further reduce and understand the data. Similar studies in arid regions (Secor *et al.*, 1983) and wetter climates (Huntley & Birks, 1979), have assisted in elucidating floristic gradients.

It has been suggested that destructive land-use practices may threaten the soils of the Karoo and the existence of the natural plant communities. Rates of soil recovery in arid regions are slow, but Webb & Wilshire (1980) record that the "recovery" trend for soil physical properties after disturbance in arid areas may be as short as 100 years. Replacement may not be important if the remaining soil contains enough nutrients to sustain initial plant growth.

It is my intention to test whether or not the chemical properties of the soils of the study area relate to the vegetation structure, and to present an alternative, testable hypothesis, on the influence which the soils have on vegetation composition.

The study area

The study area is some 40 000 km^2 in extent, and is situated in the Nama-Karoo and Grassland Biomes (Rutherford & Westfall, 1986) between 31^o - 33^o S and 24^o - 26^o E. The major towns in the study area are Graaff-Reinet, Middelburg, Cradock and Somerset-East. The study area comprises two sheets of the 1:250 000 SA Topo Series (3124 Middelburg and 3224 Graaff-Reinet), and varies in altitude from 375m at Jansenville to 2502m at Compassberg.

Triassic sandstones of the Beaufort Group are the most prominent geological formation in the

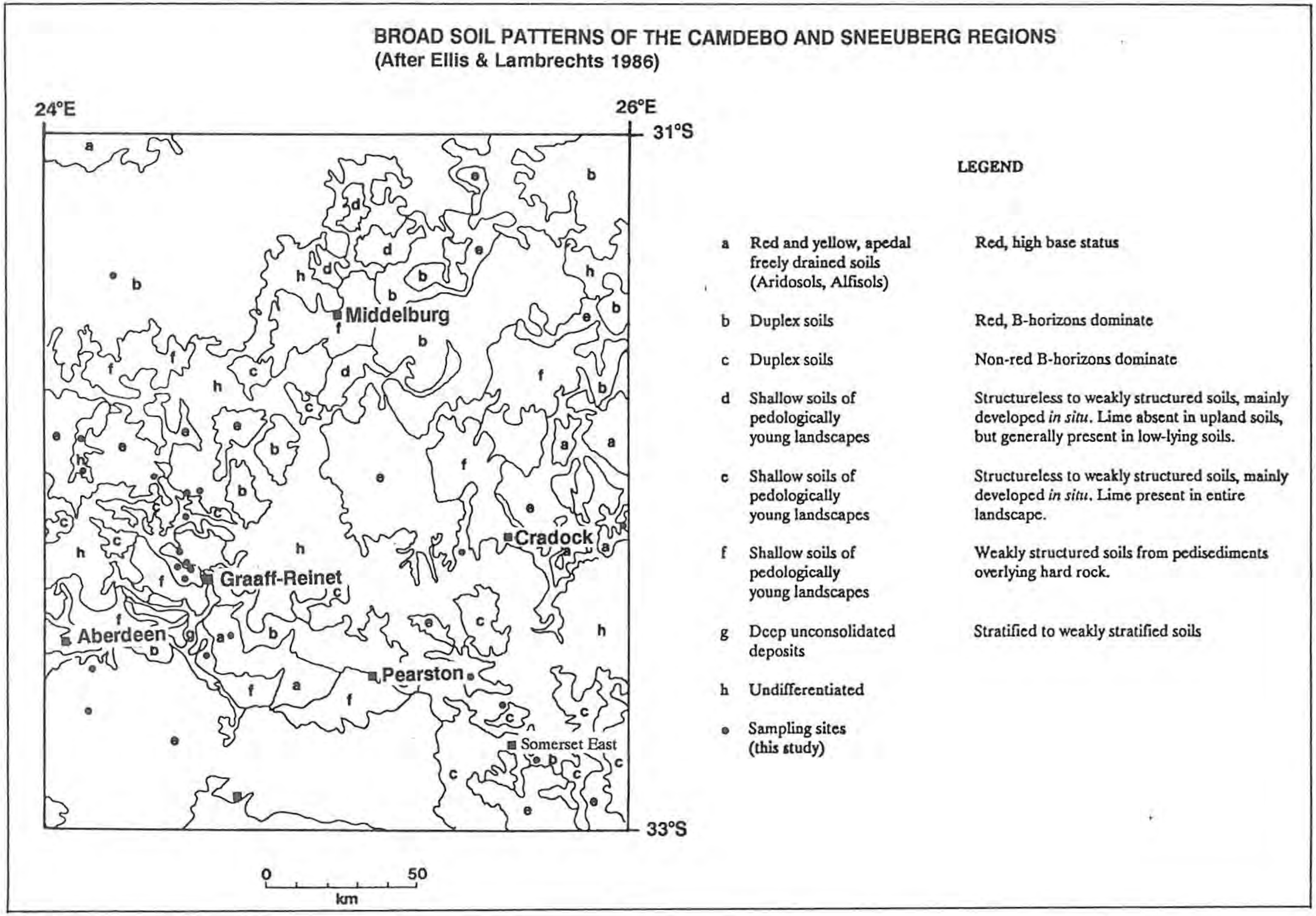

Figure 1. Broad soil patterns in the study area (after Ellis & Lambrechts, 1986), and the location of sampling sites.

study area (Visser, 1986), and these have been intruded by dolerites which give rise to an uneven topography of mesas, hillocks and sharp ridges. Deep, Quaternary alluvial deposits occur on the bottomlands where they are readily susceptible to erosion.

In common with the soils of the other arid and semi-arid regions of the world (Evenari 1985), the main soil orders represented in the Karoo are aridosols and alfisols (MacVicar *et al.*, 1977, Vorster, 1985). The aridosols contain layers of duripans within 1 metre of their surface. These calcareous hardpans were apparently formed during pluvial episodes (Evenari, 1985) when active leaching took place, such as in the flood conditions at the beginning of 1988. This happened in Australia during 1974 when the mean annual rainfall experienced by central Australia trebled (Williams & Calaby 1985).

The predominant soil types are shallow aridosols of pedologically young landscapes (Ellis & Lambrechts, 1986) which have developed under conditions of rainfall deficiency (Van der Merwe, 1941). The pediments contain structureless to weakly structured soils, mainly developed from *in situ* weathering, with lime generally present in the entire landscape (Figure 1). The presence of lime is an indication of the limited extent to which these soils have been leached (Ellis & Lambrechts, 1986).

The uplands contain rocky, shallow lithosols of the Mispah Form (MacVicar *et al.*, 1977). The weathering of the plagioclase (mainly Ca, Na, Al, Si) and pyroxene (Ca, Na) (Mg, Fe, Al) (Si, $Al)_2 O_6$ may lead to a favourable environment for plant growth. The lithosols are found in three broad categories based on the geological origin of the dominant parent material: 1) the Mispah/rock complex of sloping landforms where dolerite overlies sandstone or mudstone (Van Riet & Minnaar, 1977); 2) the Mispah soils on Beaufort series sandstone on the convex sloping landforms; 3) the Mispah soils of the high-lying or raised plateaux of flat to gently sloping landforms. In all instances, the material underlying the A-horizon is hard rock, and the soil series classification of MacVicar *et al.* (1977) did not provide adequate classification classes for the purposes of this study. Ellis & Lambrechts (1986) regard much of the study area as "undifferentiated" (Figure 1).

The climate of the study area is influenced by altitude and distance from the moderating influence of the ocean. There is a steep aridity gradient from east (591mm at Somerset East) to west (284mm at Aberdeen). The major part of the area receives summer rain (October-March). The reliability of annual rainfall (expressed as a percentage of years with rainfall greater than or equal to 85% of the mean annual rainfall) is 65-70% (Venter *et al.*, 1986). Tyson

(1986) suggests that Graaff-Reinet experiences a 12-year oscillation between wet and dry phases. Meadows *et al.* (1987) have investigated a site near the study area and have not detected any trend in the pollen record of the last 8000 years which may indicate progressive desiccation. Large temperature fluctuations (both daily and seasonal) are one of the most outstanding characteristics of the Karoo region (Venter *et al.*, 1986). The study area has a mean daily maximum temperature of 30° C in the hottest month, with a mean annual temperature of 15° C. The duration of frost at Middelburg is 158 days (Venter *et al.*, 1986), one of the longest periods experienced by stations in the region.

The hypothesized vegetation classification (Palmer, 1988), contains examples of vegetation from three phytochoria: the Dwarf Shrublands of the Nama-Karoo biome (Rutherford & Westfall, 1986); the Succulent Thicket of the Sub-tropical Transitional Thicket (Cowling, 1984); and the Grasslands and Shrublands of the Sudano-Zambezian Region (Werger & Coetzee, 1978).

The Dwarf Shrublands of the Nama-Karoo are represented by four structurally distinct formations. The term Dwarf Shrubland refers to the predominance of low-growing (<40 cm) perennial woody plants. Varying proportions of succulence and grassiness account for the distinctions between the variations. The Degraded Dwarf Shrubland, situated mainly on the deep, structureless soils of the Quaternary alluvium, are dominated by thorn trees (*Acacia karroo*), dwarf shrubs (*Pentzia, Chrysocoma, Walafrida, Felicia, Eriocephalus*) and annual grasses (*Aristida, Eragrostis*). In the un-degraded form, the Dwarf Shrublands contain species of the genera *Pentzia, Pteronia* and *Euryops*. These communities are located on the pediments on shallow, pedologically young soils.

The Grassy Dwarf Shrubland is also found on the pediments, associated with shallow soils containing a calcrete hardpan at 20-30cm from the top. Grasses in these communities include some weak perennials (*Enneapogon, Digitaria, Eragrostis, Tragus*) as well as annuals (*Aristida, Eragrostis*). The dwarf shrubs include (*Pentzia, Pteronia*) and some succulent genera (*Mestoklema, Ruschia*) with numerous geophytes.

The Succulent Dwarf Shrubland is more characteristic, containing a high proportion of leaf succulents on the deeper, pedologically young soils of the bottomlands and pediments. The succulent genera include *Mesembryanthemum, Ruschia, Delosperma, Mestoklema, Eberlanzia, Psilocaulon* and *Salsola*.

The Succulent Thicket has both a structurally and floristically distinctive composition. It consists of short to medium (1,5-3,0m) succulent shrubs of the species *Portulacaria afra* and numerous medium woody shrubs of the genera *Euclea, Rhus, Maytenus* and *Pappea*. The vegetation often totally covers the surface of a survey quadrat.

The Grasslands and Shrublands occupy the high-lying mountainous areas of the study site. They consist of bushclumps containing woody shrubs of the genera *Rhus, Grewia, Euclea* and *Diospyros*, separated from one another by grasses (*Heteropogon, Themeda, Cymbopogon, Aristida, Merxmuellera*), dwarf shrubs (*Pentzia*) and shrubs (*Euryops, Elytropappus*).

MATERIALS AND METHODS

Soil samples were collected from twenty $100m^2$ quadrats in a single operation in May 1987 (Figure 1). The quadrats were selected from the full range of plant communities recognized by Palmer (1988), and were situated predominantly in undifferentiated (Ellis & Lambrechts, 1986) soils. A sample of $100cm^3$ was collected from the surface within each quadrat using a bucket-type soil auger. The surface litter was carefully removed before the sample was taken, and the location of the sample within the quadrat was noted. The samples were placed in separate, water-tight bags for transfer to the laboratory. Within 12 hours after collection, the soil samples were prepared for soil moisture and organic content determination. 5g of soil from each sample were weighed, oven dried at 105-110 °C for 12 hours and reweighed (British Standards Institution, 1975). Moisture content (%) was calculated according to Van Rooyen (1978). Organic content (%) was determined by heating samples at 550 °C for 1-2 hours in an electric muffle furnace.

The pH of the suspension was determined using a Metrohm pH meter Model E 280 A after 20g of sieved (mesh size 2mm), air-dried soil had been transferred to beakers and 50ml distilled water added. To determine pH (KCl), 50ml of 1 mol/litre KCl solution was used instead of water. The suspension was left for 24 hours and conductivity (umhos cm^{-1}) was measured using an Electronic Switchgear Conductivity Meter Model MC-1, Mark V. Ammonium acetate (pH = 7) was used for cation extraction according to the method of FSSA (1974).

Extractable cations were removed by ammonium acetate, and the exchange material (soil) became saturated with ammonia (Chapman, 1965). Strontium nitrate solution was added to the filtrate to counteract the depressing effect of phosphate on Ca and Mg determination (FSSA, 1974). Na, K, Ca and Mg concentrations (ppm) in the filtrate were determined by atomic absorption on a Varian Techtron Atomic Absorption Spectrophotometer AA5. Available phosphorus was determined using the Bray No. 1 acid extraction procedure outlined by FSSA (1974). Particle size distribution was determined by means of pipette analysis (Day, 1965), and the air dry colour of the samples was ascertained in the laboratory using a Munsell colour chart (Munsell Color Company, 1971).

Numerical analysis of the soil characteristics

The soil data for the 20 quadrats consisted of thirteen variables (moisture content (%); organic content (%); pH (H_2O); pH (KCl); Mg; Ca; Na; K; Cond (umohs/cm); available phosphorus; sand (%); silt (%) and clay (%) (Table 1). The variables were initially standardized to zero mean and unit variance because of the different measurement units. Ordination of the samples on the basis of the soil data was carried out using principal component analysis (PCA) (Cooley & Lohnes, 1971). The correlation matrix revealed extremely high correlation between pH (H_2O) and pH (KCl) ($r=0.93$). It was thereafter decided to use only pH (H_2O) in further analyses, as these strong correlations would mask other possible interpretation of the physico-chemical gradient.

RESULTS AND DISCUSSION

The most relevant correlations are Ca and Mg ($r=0.88$), with Mg ($r=0.57$) and Ca ($r=0.65$) concentrations correlating with soil alkalinity (pH-KCl). This is a well documented phenomenon (Schroeder, 1984), but has seldom been compared to a floristic gradient. A strong positive correlation exists between available phosphorus concentration and the minerals Mg, Ca, Na and K.

The texture chart (Figure 2) indicates that many of the samples are sandy loams or loamy sands. A relationship between the floristic classification and soil surface texture in the study area is not apparent. As the plot of the first and second principal component (PC) axes did not provide any obvious relationship between vegetation classification and soil, I plotted first versus third PC axes and the pattern paralleled the vegetation classification (Figure 3). The interpretation of Figure 3 is facilitated by the provision of certain information about the loading which has been applied to the elements of each component axis (Table 2).

The samples along the first component axis have high Ca, Mg and conductivity values on the left hand side and lower values on the right. The extreme left contains minerally rich sites in the Shrubland, and on the right are the leached soils of the mesic grassland. The Grassy Dwarf Shrubland cluster displays higher Ca, Mg and conductivity levels than the Succulent Dwarf Shrubland. The higher Ca levels in the Grassy Dwarf Shrubland may be explained by the regular presence of a $CaCO_3$ (limestone) layer 20-30 cm below the surface.

Table 1. Soil variables from twenty samples in the Camdebo and Sneeuberg regions.

Relevé No.	H_2O (%)	C (%)	pH		Extractable cations (me/100g)				Cond μmhos cm^{-1}	P mg/kg	Sand	Silt (%)	Clay
			H_2O	KCl	Mg	Ca	Na	K					
131	3.4	2.0	6.7	5.2	213	415	8.3	73.0	50	10.4	70.78	10.10	19.12
193	5.5	8.0	6.2	5.0	149	560	6.1	62.3	114	10.0	86.45	6.37	7.18
199	5.0	4.0	7.1	6.0	367	905	13.0	91.0	187	5.2	65.77	21.95	12.28
217	9.9	4.0	6.1	4.9	246	525	5.7	55.3	65	8.7	69.79	13.36	16.85
219	7.5	6.0	6.4	5.0	229	435	9.6	49.9	77	19.0	71.51	13.35	15.14
230	8.6	2.0	7.0	5.6	154	280	16.6	70.7	93	7.0	83.19	10.56	6.25
258	2.7	2.0	7.1	5.8	266	480	15.7	82.3	76	19.0	71.59	12.09	16.32
261	2.2	0.0	7.4	6.3	167	540	19.6	42.3	106	20.0	87.25	4.95	7.80
266	2.9	2.0	6.7	5.6	351	525	22.2	50.7	84	13.2	83.67	8.52	7.81
267	4.6	4.0	8.0	6.5	378	760	57.5	105.3	245	8.7	73.15	11.98	14.87
268	2.8	4.0	7.4	6.0	314	630	10.0	36.1	83	11.5	83.39	16.27	0.34
269	4.1	4.0	5.8	4.4	275	695	8.7	23.6	101	10.0	81.17	8.84	9.99
270	9.2	12.0	7.8	6.9	704	1200	10.9	73.5	360	16.4	79.58	13.55	6.87
270*	13.8	36.0	7.1	6.6	880	1375	30.5	101.7	1137	7.0	82.41	8.89	8.70
271	6.5	2.0	6.1	5.1	284	530	26.6	52.0	73	8.5	76.58	6.76	16.66
272	7.2	8.0	6.2	5.1	232	720	10.0	82.8	114	8.8	67.82	22.09	10.09
273	9.5	6.0	6.4	5.5	362	810	6.9	56.1	142	5.5	81.13	13.00	5.87
274	6.2	2.0	6.3	5.4	156	340	16.1	54.0	81	7.5	79.3	38.45	12.22
275	4.3	6.0	5.4	4.3	144	220	12.6	18.9	73	8.7	98.09	2.73	4.64
279	6.1	2.0	7.5	6.4	295	780	17.8	128.1	292	25.7	71.32	10.10	18.58

* Additional sample collected inside a bushclump in the shrubland.

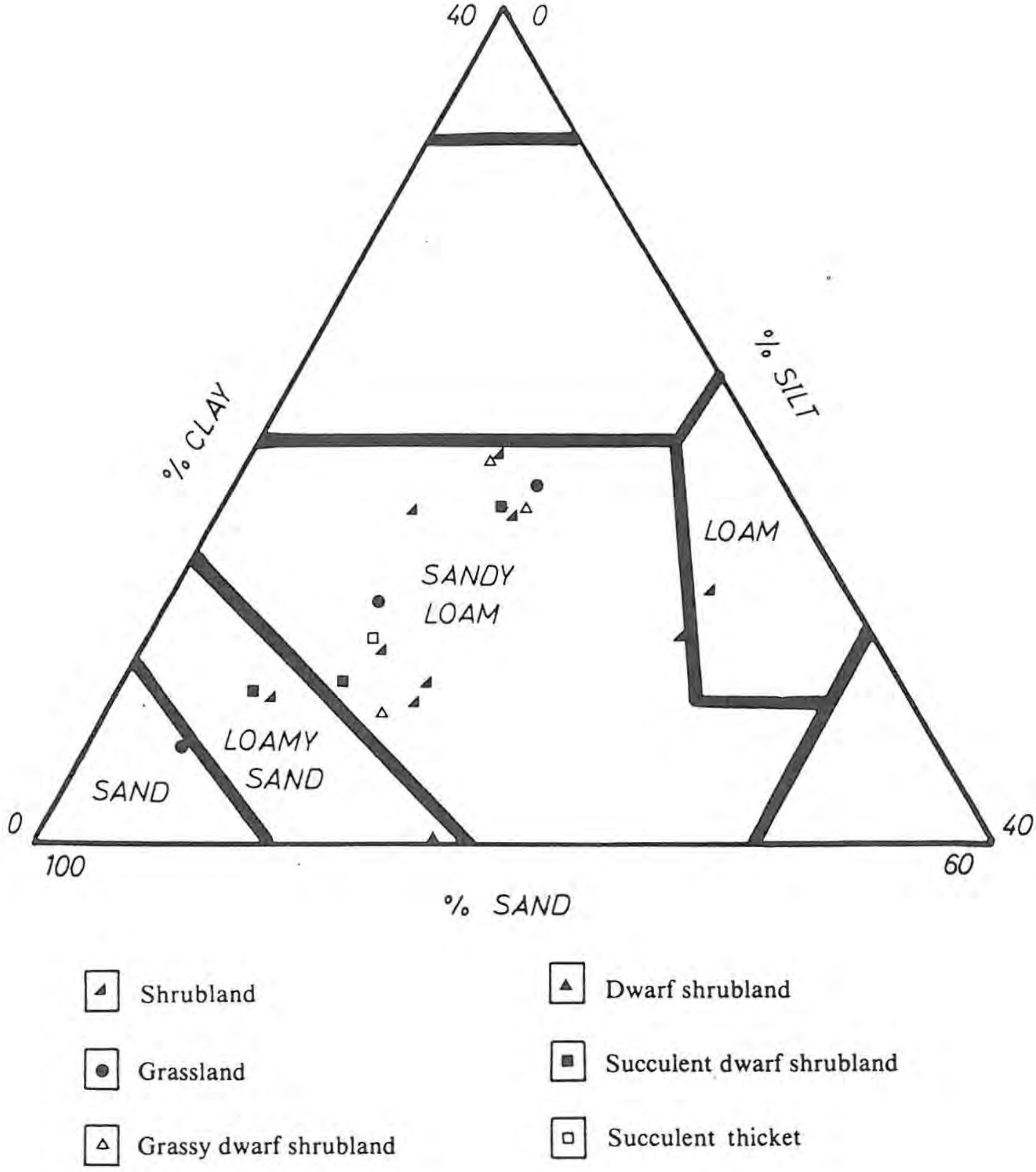

Figure 2. Soil texture chart for samples collected during the study.

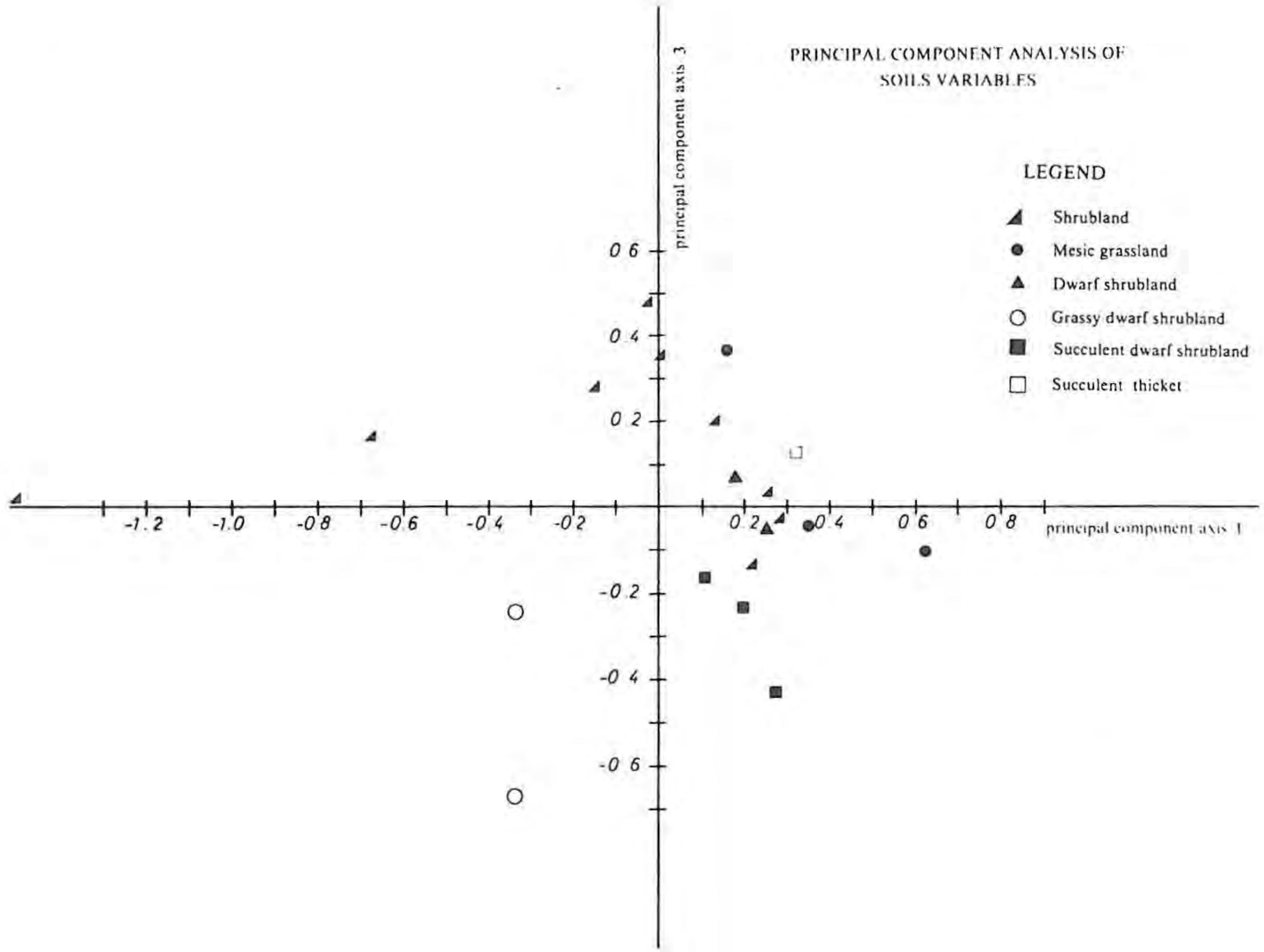

Figure 3. A plot of the first and third principal component axes for twelve soil cariables.

Table 2. (a) The percentage of total variance accounted for by each component, and (b) the loading applied to each soil factor in the first three principal components.

(a)

Component	% of total variance
1	43,5
2	21,8
3	12,6

(b)

Soil attribute	% moisture	%C	pH	Mg	Ca	Na	K	Cond	P	Sa	Si	Cl
Component 1	8	14	4	16	15	1	8	18	12	1	1	0
Component 3	13	2	12	1	2	37	2	1	2	5	21	2

The third principal component axis parallels the silt/Na/pH gradient which occurs in the ecosystem. In the upper half of the diagram, the low silt, Na and low pH samples occur with the higher Na, silt and pH levels in the lower half. The Succulent Dwarf Shrubland and the Grassy Dwarf Shrubland pediment communities are higher in Na and silt than those of the Shrubland, mesic Grasslands and Succulent Thicket and they have consistently more basic pH. The plant communities of the mountain slopes (Shrublands) and mesic Grasslands, where the rainfall is higher, are more leached. The silt fraction is lower, and pH is less basic. The moisture content of the soils of these communities was also higher. Although many of these gradients may have been expected from the field survey, the PCA has supported the classification arrived at during the floristic survey. The hypothesis that the floristic classification paralleled, among other things, a soil gradient is generally confirmed.

It should now be possible to further test this hypothesis by identifying any of the vegetation formations recognized, collecting a range of samples reflecting the floristic units within these formations, collect soil samples from these units and subject them to the same process of analysis. This study does has not attempted to provide a comprehensive appraisal of Karoo soil chemistry, but rather to examine the broad differences between disparate plant communities.

Pedestal formation around perennial dwarf shrubs, which is the most obvious observable sign of excessive erosion, may be a consequence of progressive sediment accumulation. During the passage of weathered material to the bottomland, the sediment is deposited around the dwarf shrubs on the pediments. Large quantities of Ca and Na from the plagioclase and pyroxene minerals in the doleritic parent material on the rocky slopes are continuously transported to the pediments. This may account for the high Ca and Na levels experienced in these pediment soils.

The presence of dolerite dykes adjacent to sandstone and mudstone parent material on the pediments, ameliorate the otherwise alkalkine conditions, giving rise to an *Eberlanzia*-dominated Succulent Dwarf Shrubland. The ameliorating influence of the dolerites is also found on the concave slopes where *Portulacaria afra* occurs. Conditions of moderate acidity appear to favour the succulent species, however, this hypothesis needs further investigation.

The determination of air dry soil colour (Figure 4) revealed a gradient from the dark brown soils (10YR 3/2) of the high-lying areas to the reddish brown soils (5 YR 5/6) of the bottomlands (Table 3). This parallels the gradient from the high altitude Grasslands and Shrublands to the low-lying Succulent Dwarf Shrublands.

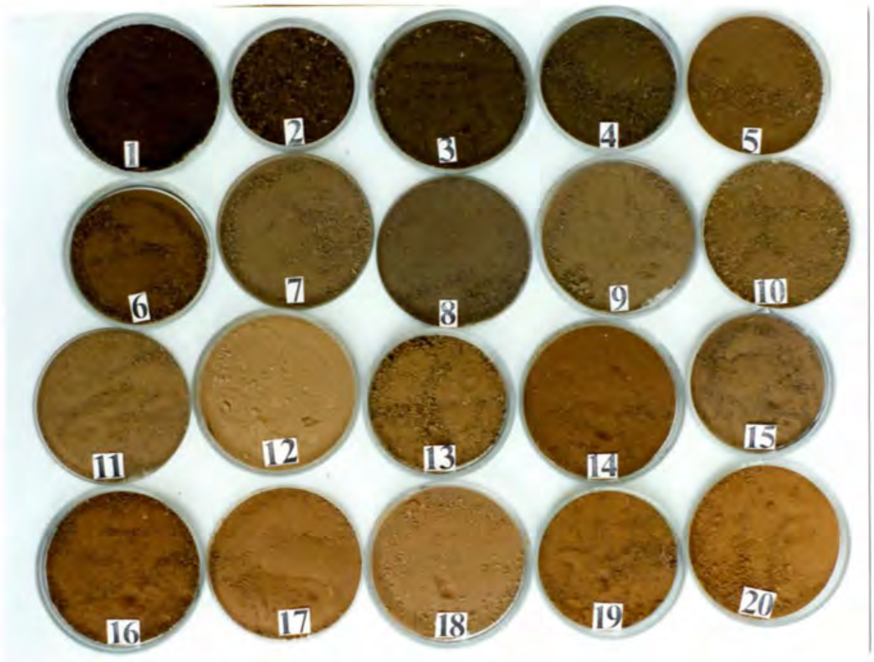

Figure 4. Soil colour gradient for samples collected during this study. See Table 3 for details on the vegetation and site environmental variables of the numbers 1 to 20.

Table 3. Details of the site variables and vegetation type along the soil colour gradient (Figure 4) in the Camdebo and Sneeuberg regions of the Nama-Karoo Biome.

Number in Figure 4	Air-dry colour	Relevé number	Vegetation type	Altitude (m)	Geology
1	10YR3/2	273	Shrubland	1667	Dolerite
2	10YR3/2	270	Shrubland	1348	Dolerite
3	10YR3/2	270*	Shrubland	1348	Dolerite
4	10YR3/3	199	Shrubland	1318	Dolerite
5	10YR4/3	272	Shrubland	1639	Dolerite
6	10YR4/4	217	Grassland (montane)	1500	Sandstone
7	10YR5/3	219	Shrubland	1576	Sandstone
8	10YR5/2	275	Grassland (montane)	1450	Sandstone
9	10YR5/2	274	Grassland (lowland)	750	Sandstone
10	10YR5/3	271	Dwarf shrubland (montane)	1310	Dolerite
11	10YR5/4	230	Grassy dwarf shrubland	1300	Dolerite
12	7.5YR5/4	282	Succulent dwarf shrubland	750	Alluvium
13	10YR5/4	269	Succulent thicket	909	Dolerite
14	7.5YR4/4	193	Dwarf shrubland (montane)	1640	Sandstone
15	7.5YR4/4	261	Succulent dwarf shrubland	630	Sandstone
16	7.5YR4/4	279	Grassy dwarf shrubland	1000	Alluvium
17	7.5YR5/6	267	Grassy dwarf shrubland	750	Sandstone
18	7.5YR5/4	258	Succulent dwarf shrubland	742	Alluvium
19	5YR5/6	268	Dwarf shrubland	850	Dolerite
20	5YR5/6	266	Succulent dwarf shrubland	790	Alluvium

*Sample from inside the bush-clump.

Table 4. A comparison of the soil characteristics from five broadly synonymous soil types in the Nama-Karoo and other biomes (Rutherford & Westfall, 1986) in South Africa.

Biome	Nama-Karoo			Savanna	Grassland	Fynbos
Formation*	1	1	2	3	4	5
Author**	a	a	b	c	d	e
Sample No.	6	6	258	58	183	3
Depth (cm)	0-6	6-25	0-30	0-30	0-30	0-30
Sand (%)	84.7	68.4	71.5	70.0	68.0	-
Silt (%)	5.8	6.6	12.1	16.0	15.0	-
Clay (%)	9.1	24.8	16.3	14.0	18.0	-
pH (H_2O)	8.3	8.0	7.1			7.7
pH (KCl)	-	-	5.8	6.8		
Na (me/100g)	10	10	15.7	9.6	-	154
K "	50	20	82.3	87.4	71.7	77
Ca "	510	960	480	737	350	470
Mg "	80	200	266	269	260	1330
S-value	650	1190	844	1103	-	2030
CEC	600	1190	-	-	-	-
Conductivity	-	-	76	99	-	210
% oxidizable C	0.3	0.3	2	-	-	4
% moisture	-	-	2.7	3.1	-	-
P (mg/kg)	-	-	19	-	5	4
Soil form	Glenrosa		Swartland	Mispah	Sterkspruit	-
Soil texture***	l/sa	s/cl/lm	sa/lm	s/cl/lm	-	sa/lm
Dominants	?	?	*Eberlanzia*	*Cymbopogon*	*Heteropogon*	*Cussonia*
				Phyllanthus	*Themeda*	

* (1) dwarf shrubland; (2) succulent dwarf shrubland; (3) succulent thicket; (4) lowland grassland; (5) dune fynbos

** (a) Ellis & Lambrechts (1986); (b) This study ; (c) Palmer *et al.*(1988); (d) Bosch (1977); (e) Van der Merwe (1976)

*** (l/sa) loamy sand; (s/cl/lm) sandy clay loam; (sa/lm) sandy loam.

When comparing the soils of the Karoo with the soil data from other biomes (Table 4), it is apparent that the pediments of the Karoo are covered by a thin layer of minerally-rich, eutrophic soils. Soil pH is higher than for any of the other biomes, and this appears to be a consequence of high Na levels at or near the surface. The high mineral and base status is further aggravated by low precipitation rates and soil surface compaction. Leaching of minerals and salts is hampered by the presence of impermeable rock at shallow depths, as well as the presence of the $CaCO_3$ layer. The high sand fraction for soils of the pediments of the study area appears to be one of the major features distinguishing Karoo soils from those in other biomes (Table 4).

In contrast to the prevailing interpretation, it would seem that the soils of the pediments in the study area are not severely degraded. The soil profiles examined during this study showed an integrity of structure which may be associated with well-preserved conditions. The soils contain sufficient nutrients to sustain plant growth, and it is the precipitation events which determine fluctuations in production levels.

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A qualitative model of vegetation history in the eastern Cape midlands, South Africa.

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ABSTRACT

A qualitative model of the vegetation history during the glacial-interglacial sequence in the Graaff-Reinet region of the eastern Cape is presented. Using a descriptive approach, the distribution patterns of 68 taxa, which are differential species for Karoo Shrublands, Succulent Thicket and Karoo Dwarf Shrublands, are investigated relative to major southern African biomes. The results indicate that a large proportion of the differential species in the phytosociological classification show strong affinity with Grassland and Savanna Biomes. Three species groups encountered in the Dwarf Shrublands show strong affinities with the Nama-Karoo biome. The differential species of the Succulent Thicket have a predominantly subtropical distribution. Using an historical approach, the palaeoenvironment of the region during the past 20 000 years is discussed briefly. On the basis of the descriptive and historical perspectives, the following hypothesis is presented:

The general vegetation history of the eastern Cape midlands is a product of comparatively recent climatic change. The Succulent Thicket may have become established on edaphically favourable sites in the ameliorating conditions of the warmer, wetter Holocene subsequent to the Last Glacial Maximum. The Dwarf Shrubland and Succulent Dwarf Shrubland are depauperate in relation to communities in other southern African biomes, but the relatively large number of endemics suggests a long history in the region. Their differential species groups occur under arid conditions, accompanied by soils with high base and fertility status. The Dwarf Shrublands may have been more extensive during the drier glacial times on those sites currently occupied by Shrubland. The Shrublands display the expected affinity with the Grassland and Savanna Biomes. The small number of endemics suggest that these communities may have occupied the region in the period since the Last Glacial Maximum. Species with Succulent Karoo Biome affinity are poorly represented.

Introduction

The eastern Cape, South Africa, has been identified as a region of phytogeographical interest (Gibbs Russell & Robinson, 1981; Cowling, 1983; Everard, 1987; Lubke *et al.* 1988). It represents the tension zone between four phytochoria, namely the Karoo-Namib (Werger, 1978), Afromontane (White, 1978), Tongaland-Pondoland (Moll & White, 1978) and the Sudano-Zambezian region (Werger & Coetzee, 1978). Gibbs Russell & Robinson (1981) suggest that the physiographic and climatic variability in the eastern Cape (Tyson, 1986; Vogel, 1988) results in spatial and temporal heterogeneity in the vegetation. Gibbs Russell & Robinson (1981) found that the distribution of large numbers of taxa end in this region, confirming that the eastern Cape is the boundary between a number of phytochoria. The region has not developed a distinctive flora, probably as a consequence of the variability of the environment in which selection for "generalist" genotypes have been favoured (Gibbs Russell & Robinson 1981). Werger (1978, 1983) and White (1983) regard the extensive arid and semi-arid areas of the south-western part of southern Africa as the Karoo-Namib biogeographical region. This region is divided by Rutherford & Westfall (1986), using an objective categorization based on dominant and co-dominant life forms, into three biomes, namely the Nama-Karoo, Succulent Karoo and Desert Biomes (Figure 1).

Werger & Coetzee (1978) report that the border area between the Karoo and the Sudano-Zambezian Grasslands of the Highveld is floristically transitional. It has been suggested that Karoo-Namib species intruded into the Grasslands, enhanced by overgrazing by domestic livestock (Acocks, 1975; Werger, 1973, 1983; Jarman & Bosch, 1973). Werger & Coetzee (1978) and more recently Roux & Theron (1987) suggest that evidence for this intrusion can be found in the diaries and travel accounts of the early-day travellers. The late eighteenth and nineteenth centuries were generally wetter than the early part of the twentieth century (Tyson 1986, Vogel 1988), and both wet and dry conditions are reported in the writings of early travellers (Skead 1988).

Biogeography allows the phytosociologist to explore the vegetation history of the region under consideration. A biogeographic study is a multi-stage decision-making process in which quantitative and computer methods are used iteratively to improve our understanding of the distribution of a flora (Crovello 1981), in which the fundamental unit is the taxon (Cowling, 1983). The steep environmental gradients occurring in the Camdebo and Sneeuberg regions make it an excellent natural laboratory in which to study the ecological factors determining biogeographic limitation (Cowling 1982). I wish to assess the history of the differential taxa in order to further understand the relationship between the species groups identified in the

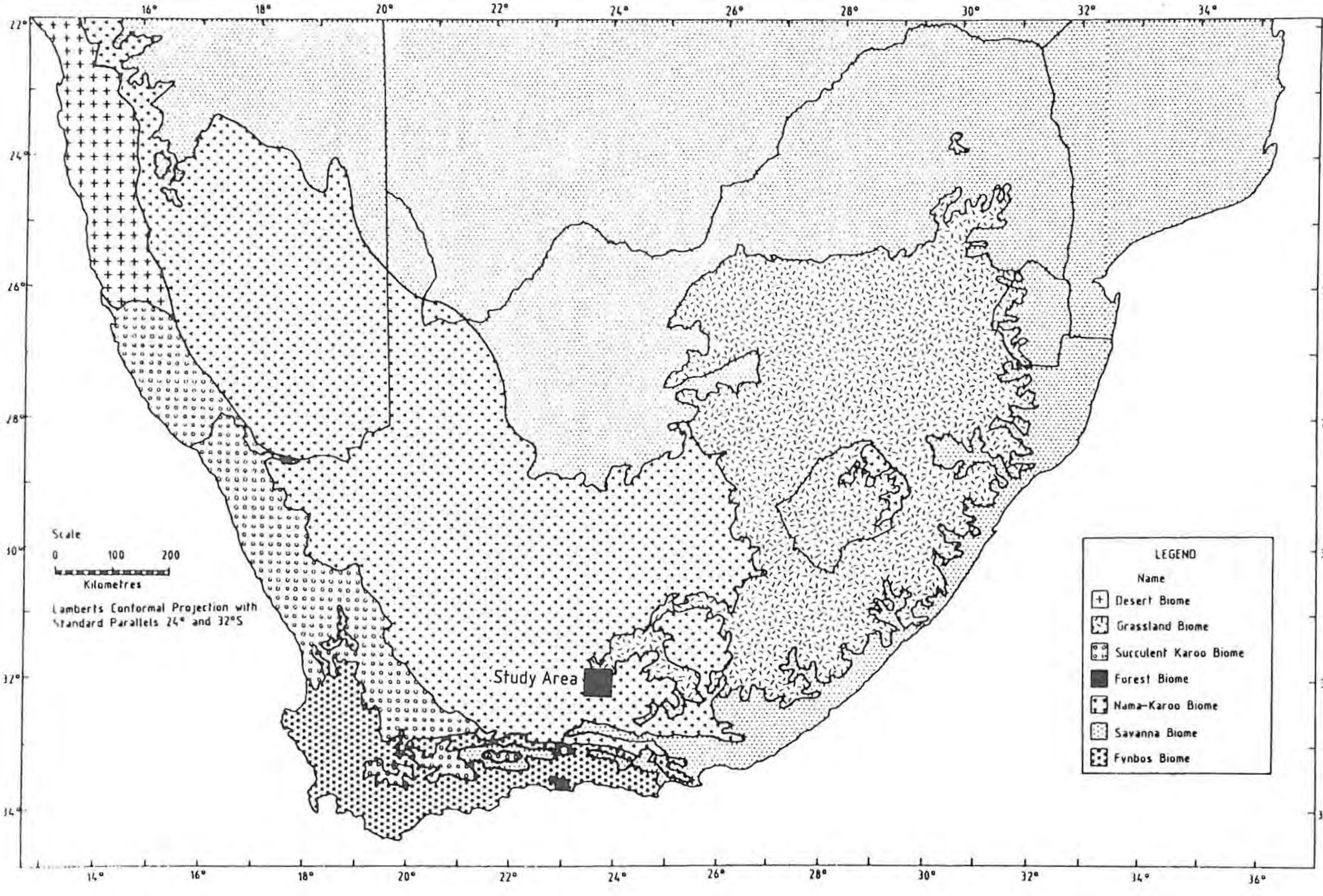

Figure 1. The biomes of southern Africa (after Rutherford & Westfall, 1986).

syntaxonomic treatment (Palmer, 1988c). I use the biome concept in favour of the phytochorion, since Rutherford & Westfall (1986) have provided a objective categorization of the biomes of southern Africa which is lacking in the subjectively derived phytochoria (Hilton-Taylor, 1987).

I develop a testable qualitative model of vegetation history in the Camdebo and Sneeuberg regions using the results of the descriptive study. The model is tested using perspectives of the palaeoclimate, the phytochorological affinities of the contemporary vegetation and the patterns of endemism shown by communities in the region.

The Study Area

A descriptive study of the vegetation of the Karoo Nature Reserve, Graaff-Reinet, was undertaken (Palmer 1988a, 1988b), forming part of a regional assessment of the flora of the Nama-Karoo biome (Palmer, 1988c). Total floristic information was collected from 78 quadrats (100 m^2) and synthesized into an hierarchical classification using the methods of the Zürich-Montpellier school of phytosociology. Details of this syntaxonomic hierarchy and environmental relationships are presented in Table 1. The nature reserve occurs within the Nama-Karoo Biome (Rutherford & Westfall, 1986). Acocks (1975) recognized four karroid Veld Types in and adjacent to the study area, namely False Karroid Broken Veld, Succulent Mountain Veld, False Central Lower Karoo, False Upper Karoo and one Pure Grassveld Type (Karroid *Merxmuellera* Mountain Veld).

The Shrublands occupy the high-lying mountainous areas of the study site. They consist of bushclumps containing woody shrubs of the genera *Rhus, Grewia, Euclea* and *Diospyros*, separated from one another by Grasslands (*Heteropogon, Themeda, Cymbopogon, Aristida, Merxmuellera*) or by Dwarf Shrublands (*Pentzia, Euryops, Elytropappus*).

The Succulent Thicket has both a structurally and floristically distinctive composition. It consists of short to medium (1,5-3,0m) succulent shrubs of the species *Portulacaria afra* and numerous medium woody shrubs of the genera *Boscia, Ehretia, Carissa, Rhus, Maytenus* and *Pappea*.

The Dwarf Shrublands of the study area are dominated by low-growing (<40 cm) perennial woody plants. Varying proportions of succulence and grassiness account for the distinctions between the communities, with species of the genera *Pentzia, Pteronia* and *Euryops* being dominant. The grassy form is located on the pediments on shallow, pedologically young soils containing a calcrete hardpan at 20-30cm from the surface. Dominant grasses which are

Table 1. Site environmental variables and vegetation of eight type relevés in the Karoo Nature Reserve.

Class	Order	Species Groups Present	Altitude (m)	Geology	Soil Form	Soil colour	Mean annual rainfall (mm)
Karoo Shrublands	Shrubland on rocky slopes	1,2	1667	Dolerite	Mispah	10YR3/2	560
	Grassy Shrubland	3	1565	Dolerite	Mispah	10YR3/2	450
Subtropical Thicket	Succulent Thicket	4	909	Dolerite/ mudstone	Mispah-rock complex	10YR5/4	400
Karoo Dwarf Shrublands	Dwarf Shrubland	5	850	Sandstone	Swartland	5YR5/6	300
	Succulent Dwarf Shrubland	6,7,8	790	Sandy alluvium	Nyoka-Dudfield	5YR5/6	250
	Grassy Dwarf Shrubland	5	770	Sandstone	Swartland	5YR5/6	350
	Degraded Dwarf Shrubland	5,7	840	Alluvium	Various	5YR5/6	350

encountered in this community include some weak perennials (*Enneapogon, Digitaria, Eragrostis, Tragus*) as well as annuals (*Aristida, Eragrostis*).

The Succulent Dwarf Shrubland contains a high (40-50%) cover of leaf succulents and occurs on the deeper, pedologically young soils of the bottomlands and pediments. The succulent genera include *Mesembryanthemum, Ruschia, Delosperma, Mestoklema, Eberlanzia, Psilocaulon* and *Salsola*.

Methods

A list of 68 taxa, comprising the differential species for each of the communities, was compiled. Distribution maps (Appendix Maps 1) were prepared from herbarium records in the National Herbarium (PRE), the Albany Museum Herbarium, Grahamstown (GRA) and from the PRECIS database (Gibbs Russell & Gonsalves, 1983; Magill *et al.*, 1983). The distribution points were based on the quarter-degree square (Edwards & Leistner, 1971) and a total of 7 466 entries were considered. Distribution maps in monographs of recently revised taxa were also consulted. Voucher specimens of taxa used in the analysis, housed in GRA, the herbarium on the Karoo Nature Reserve, and PRE, are listed in Palmer (1988b).

In the preparation of distribution maps for the 68 selected taxa, entries from the PRECIS database were selected in the following manner:

i) in the case of rare or poorly collected species all the records were used to prepare the distribution maps.

ii) in the case of common species, about 130 randomly selected entries from PRECIS were regarded as an adequate sample of the distribution of a species.

The biome map of Rutherford & Westfall (1986) was redrawn to match the scale of the distribution maps. When a record occurred within one of these suggested biomes it was recorded as a 'strike'. If it occurred at the boundary between two biomes, or in one of the biomes not under consideration its distribution was regarded as 'uncertain'. The number of strikes for each species in each biome was determined. A matrix (Table 2) was prepared of the distribution frequencies of each species in each biome. The mean distribution frequency of each species group for each biome was calculated. The species groups in Table 2 have been arranged to parallel the aridity gradient which was identified in the phytosociological classification (Palmer, 1988a).

The total flora of the region was estimated from Grobler (undated), Hobson (1984), Palmer

Table 2. The biogeographical affinity of the differential species of the plant communities of the Karoo Nature Reserve. Values represent the relative proportion of the sample (n) which had been collected in each of five biomes (Rutherford & Westfall, 1986). SK = Succulent Karoo, G = Grassland, NK = Nama-Karoo, F= Fynbos, S = Savanna, U = uncertain or other biome; N = number of quarter-degree squares in which the species was recorded; n = sample size.

	BIOME							
	SK	G	NK	F	S	U	N	n
Species group 1								
Ehrharta calycina	25	3	12	39	14	7	130	333
Rhus undulata var. *undulata*	9		13	34	19	25	52	122
Euclea undulata var. *undulata*	9	9	9	18	47	8	65	111
Euryops spathaceus		11	11	18	44	16	27	30
Walafrida geniculata		8	47	11	34	0	47	56
Aloe broomii var. *tarkaensis*		100				0	3	4
Buddleja saligna		26	13	20	39	2	70	82
Olea europeae subsp. *africana*		21	6	15	52	6	80	124
Maytenus polycantha		25	20		22	33	62	90
Eragrostis chloromelas		57	12	4	25	2	145	359
Relative contribution of each biome to the group	4	23	14	16	30	13		
Species group 2								
Heteropogon contortus		29	19	5	44	3	135	511
Digitaria eriantha		29	22	5	42	2	152	727
Cymbopogon plurinodis		30	15	4	46	5	160	339
Hibiscus pusillus		30	16	4	48	2	73	95
Themeda triandra		33	12	16	38	1	196	695
Sporobolus fimbriatus		26	19	4	46	5	160	306
Lantana rugosa		22	14		59	5	95	114
Grewia occidentalis		37	7	9	48		114	120
Diospyros austro-africana	9	39	22	23	5	2	74	110
Becium burchellianum		33	33		33	1	18	31
Relative contribution of each biome to the group	1	31	18	7	41	2		

Table 2 (continued)

	BIOME							
	SK	G	NK	F	S	U	N	n
Species group 3								
Rhus erosa		56	36			8	44	69
Merxmuellera disticha		41	25	13	10	11	80	151
Mestoklema tuberosum			50		33	17	18	20
Felicia hyssopifolia subsp. *polyphylla*		16	16	50	18	12	16	
Sutera mollis		46	27		27		22	22
Relative contribution of each biome to the group		32	31	13	14	10		
Species group 4								
Pappea capensis		15	9		63	13	91	101
Portulacaria afra		14	9	4	73		22	33
Carissa haematocarpa	18		30	12	21	19	33	38
Rhus refracta		5	26	5	64		19	31
Aloe ferox		40	8	22	14	16	35	56
Boscia oleoides		15	37	3	44	1	27	31
Peliostomum origanoides			71		29		3	7
Rhoicissus tridentata		28	7	6	54	5	110	145
Panicum maximum		37	11		51	1	135	418
Crassula ovata		24	13	11	44	8	45	60
Indigofera heterophylla				35	47	18	17	17
Sporobolus nitens		16			66	8	48	84
Ehretia rigida		27	9		59	5	75	117
Grewia robusta		10	43	2	24	21	30	44
Rhus longispina			16	24	48	12	25	34
Rhigozum obovatum		15	48		23	14	52	70
Relative contribution of each biome to the group	1	15	21	8	44	11		
Species group 5								
Felicia muricata		31	18	6	39	6	120	135
Protasparagus suaveolens		33	15	13	37	2	90	107
Senecio radicans	10	21	24	13	24	8	37	48
Rosenia humulis			66		24	10	45	62
Sutera halimifolia	3	23	51		23		35	59
Relative contribution of each biome to the group	3	22	35	6	29	5		

Table 2 (continued)

	BIOME							
	SK	G	NK	F	S	U	N	n
Species group 6								
Pachypodium succulentum			47	8	36	9	36	42
Blepharis capensis			30	30	19	21	26	41
Cadaba aphylla		5	35	8	52		60	84
Salsola aphylla	16		50	18		16	60	187
Relative contribution of each biome to the group	4	1	**41**	16	27	11		
Species group 7								
Bulbine abyssinica		57			30	13	49	80
Eberlanzia spinosa	21		69			10	29	49
Polygala hottentotta		41	7		47	5	65	68
Haworthia viscosa			71			29	7	9
Eriocephalus africanus	12	6	6	43	10	23	48	87
Anacampseros telephiastrum	8	16	42	25	8	1	12	12
Senecio acutifolius			100				4	5
Trichodiadema pygmaeum.		12	67	9	12		24	32
Euryops anthemoides subsp. *astrotrichus*			80		20		5	6
Protasparagus acocksii		50	50				2	2
Sarcocaulon camdeboense			100				10	14
Felicia filifolia		47	17	8	23	5	67	104
Relative contribution of each biome to the group	3	19	**51**	7	11	9		
Species group 8								
Lepidium divaricatum		21	13	5	37	24	38	47
Zygophyllum retrofractum	31		53			16	32	33
Galenia sarcophylla	20		58		12	10	40	97
Mesembryanthemum karrooense			100				1	1
Aptosimum procumbens	5	18	51		26		60	91
Psilocaulon articulatum			85			15	7	8
Relative contribution of each biome to the group	9	7	**60**	1	13	10		

(1988b) and listings from the PRECIS database.

Results

The Descriptive Approach

In the descriptive study of the Karoo Nature Reserve, I recognized eight species groups (Figure 2) which differentiate the plant communities (Palmer, 1988a).

Species group 1. This group contains the differential species of the Shrublands on rocky slopes of moderately high altitude (1 300-1 600 m). Woody shrubs (*Euclea undulata, Buddleja saligna, Olea europaea*) have the largest proportion of their distribution in the Savanna Biome (39-52%), with *Rhus undulata* var. *undulata* and *Ehrharta calycina* displaying Fynbos and Succulent Karoo affinitities respectively. The distribution patterns of *Eragrostis chloromelas* reflects strong Grassland affinity, with the endemic *Aloe broomii* completely restricted to the Grassland Biome. The affinity with the Savanna Biome (30%) corresponds with the structural attributes of the community, and moderate representation of Fynbos and Nama-Karoo elements suggests that these are less important components of the Shrubland.

Species group 2. This species group comprises the differential species of the Shrubland on convex stoney slopes and contains a relatively high proportion of species with a distribution in the Savanna (41%) and the Grassland Biomes (31%). Relatively few taxa show any strong distributional affinity with the Nama-Karoo Biome (18%). The grass taxa in this group are predominantly C4 grasses (Vogel *et al.*, 1978; Cowling, 1983).

Species group 3. The communities which contain this group are located on the high altitude, rocky slopes of the Sneeuberg range, and have strongest affinity with the Grassland and Nama-Karoo Biomes. The bushclumps consist mainly of *Rhus erosa*, with the grassy inter-clump cover dominated by species with strong Grassland affinity (*Merxmuellera disticha*). The small sample size detracts from the reliability of pattern interpretation.

Species group 4. This is the largest species group, containing the differential species of the Succulent Thicket. The analysis reveals strong affinity with the Savanna of Rutherford & Westfall (1986) with a mean distribution frequency of 40% for the 16 species in the group. A very wide range of life forms is encountered in the species under consideration, from leaf succulents to single-stemmed shrubs. There were no regional or local endemics present in this species group.

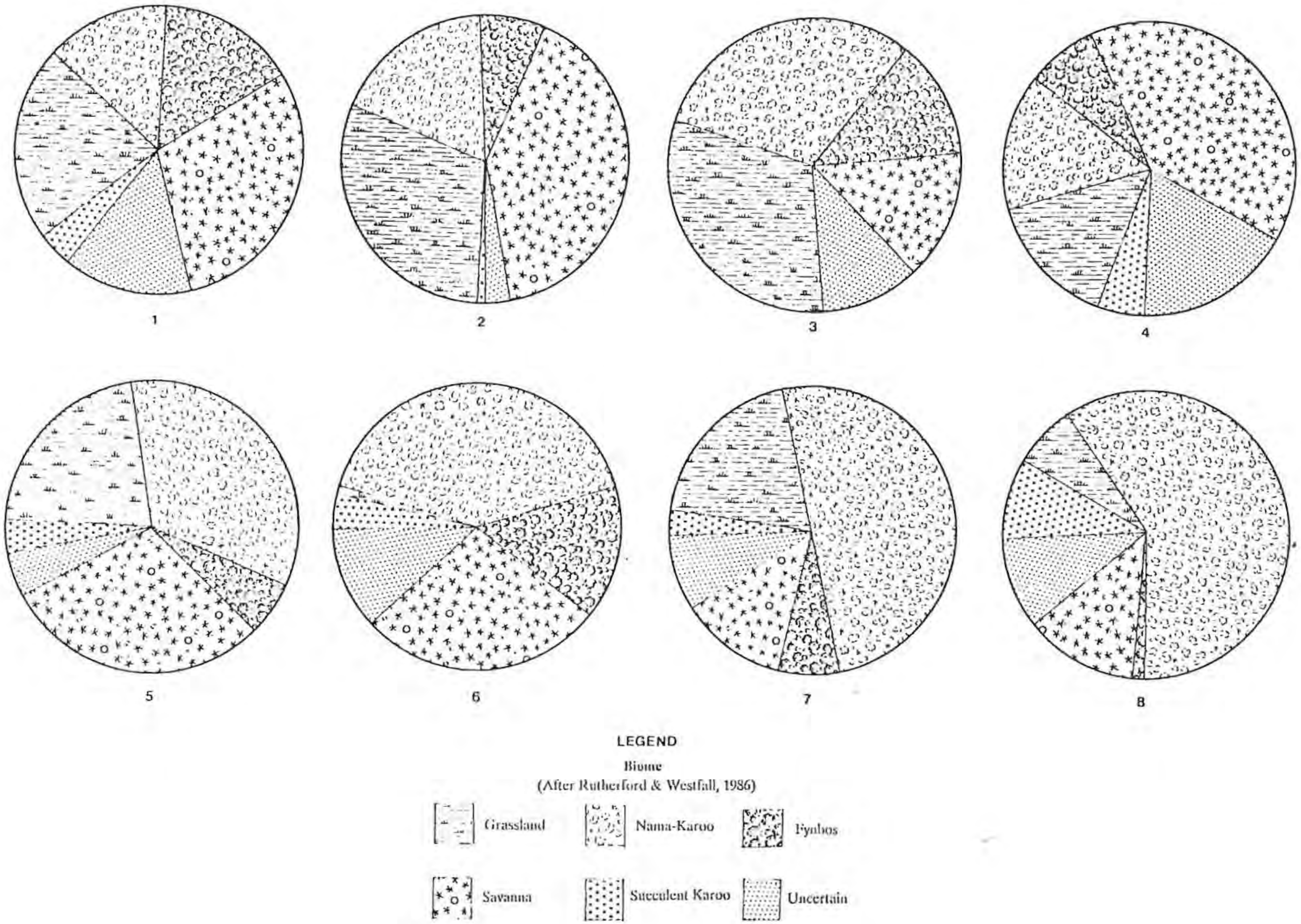

Figure 2. Phytochorological spectra for differential species groups (1-8) on the Karoo Nature Reserve.

Species group 5. This species group, comprising the differential species of the Dwarf Shrublands, displays moderate affinity with Grassland, Nama-Karoo and Savanna Biomes. Although a small group (5 species), the species have a wide distribution and are abundant in the study area.

Species group 6. This group contains the differential species for the Succulent Dwarf Shrubland and consists mainly of Nama-Karoo endemics, with some species displaying Savanna affinity. The plant communities containing this group are encountered on the pediments, with shallow (15-30 cm) moderately alkaline soil.

Species group 7. This group of twelve species contains the differential species of a variation of the Succulent Dwarf Shrubland. It is largely endemic to the Nama-Karoo, with the exception of *Polygala hottentotta* and *Bulbine abyssinica*. The species group contains leaf succulents, dwarf shrubs and geophytes. Four Nama-Karoo endemics are present, namely *Sarcocaulon camdeboense, Euryops anthemoides* subsp. *anthemoides, Senecio acutifolius* and *Haworthia viscosa*. It is the presence of this endemic group which contributes to the high mean distribution frequencies for Nama-Karoo. This species group occurred extensively in quadrats surveyed by Palmer (1988a) and must be regarded as an integral component of the vegetation of the Camdebo region of the Nama-Karoo.

Species group 8. This is the differential species group of one variation of the Succulent Dwarf Shrubland and covers a relatively small area of the Camdebo. The plant communities which are characterized by this group occur on deep (1,0 - 3,0 m) red-brown soils with moderate to high pH. The differential species are all low-growing, perennial dwarf shrubs and leaf succulents. These are Nama-Karoo endemics, suggesting that a succulent flora may have developed independently relative to the Succulent Karoo Biome.

The historical approach

Using the approach of Cowling (1986), I propose explanations of the vegetation history in the region. I focus on the period since the Last Glacial Maximum (18 000 BP) to "illustrate a hypothetical scenario in a Pleistocene glacial-interglacial sequence" (Cowling, 1983).

Palaeoclimate and vegetation change

The interpretation of evidence from diverse sources provides an interesting scenario of the palaeoclimate of the sub-continent (Deacon & Lancaster, 1988). The period since the Last Glacial Maximum (LGM) of the Late Pleistocene provides the most comprehensive and accurate evidence. This evidence has been accumulated largely out of a need to understand the conditions underwhich *Homo sapiens* inhabited the southern tip of Africa (Deacon *et al.*, 1984a). It is also an extremely important period in the evolution and diversification of the present-day flora in the region (Goldblatt, 1978; Axelrod & Raven, 1978). It emerges from numerous sources (Klein, 1980; Scott, 1983; Avery, 1984; Butzer, 1984; Scott, 1984; Tyson, 1986) that the Late Quaternary has witnessed repeated and significant changes in climate, with the harshest conditions in the last 130 000 years being experienced at the time of the LGM (Deacon *et al.*, 1984a, Deacon & Lancaster 1988).

Very little palaeoclimatic evidence has been provided for the Nama-Karoo (Deacon & Lancaster, 1988) and I have examined evidence from outside the study area. Oxygen isotope ratios from stalagmites in the Cango Caves (265 km to the south east of the study area) put the date of the LGM at 18 000 BP (Talma & Vogel in Tyson, 1986). Prior to the LGM, from 60 000 to 18 000 BP, Scholtz (1986) presents evidence for cold, dry conditions, ameliorating slightly at 22 000 BP, when "karroid scrub" vegetation predominated on the valley floors. Deacon *et al.* (1984a) and Deacon & Lancaster (1988) infer from the Cango Cave speleothem that the temperature was 5°C lower than at present. The prominence of the bush Karoo rat (*Otomys unisulcatus*) remains, the dominance of composites and the absence of woodland taxa in the charcoal samples collected at Boomplaas Cave (5 km from the Cango Caves) are indicators that drier conditions prevailed (Deacon *et al.*, 1984a). Scholtz (1986) suggests from an analysis of charcoal from the Boomplaas cave, that conditions were "cold and dry throughout the year; scrub vegetation and Grassland favoured".

The most dramatic event recorded by Scholtz (1986) is the amelioration of the climate after the LGM between 17 000 and 14 000 BP. The climate during this time was such that a "range of trees and large shrubs could grow in the valley". These included species of *Olea, Rhus, Euclea* and *Acacia*. Xylem analysis indicates that the period between 14 000 and 12 000 BP was the most mesic period since the Last Glacial Maximum. "The most prominent event recorded in the Holocene is the recent expansion of *Acacia karroo*" (Scholtz, 1986).

Further evidence for the mesic nature of the immediate post-LGM climate comes from small mammal remains (Klein, 1984). Distal humerus "breadths" (DHB) of the Cape mole rat remains (*Bathyergus suillus*) from excavations at Die Kelders were longer during the period 14 000 to 9 800 BP than in remains identified from periods before or after. Comparative measurements from contemporary Cape mole rat populations living in wet and dry conditions, show that the DHB is larger in the former population (Klein, 1984).

Deacon *et al.* (1984b) report an increase in the water levels in the Makgadikgadi Depression between 12 000 and 11 000 BP. Elsewhere in the Kalahari, there is a considerable body of evidence suggesting more effective precipitation during this period, followed by desiccation (Lancaster, 1979). In the Boomplaas site, woodland taxa (*Olea, Rhus*) appeared around 13 000 BP. Thicket taxa (*Maytenus/Pterocelastrus, Euclea/Diospyros*) become common around 10 000 BP. These data possibly represent a pulse of colonization of the region by taxa with strong sub-tropical and tropical affinity. The charcoal data must be interpreted with some caution as they could be skewed by the preferences of the hunter-gathers for certain woody species and on the site being occupied by *Homo sapiens*.

A cooler and drier palaeoenvironment is reported from the Winterberg site of Meadows & Meadows (1988) around 12 500 BP. This evidence suggests that the condition of high precipitation was of short duration, followed by drier, cooler conditions which ameliorated from 10 000 BP. onwards.

Scholtz (1986) suggested that these drier conditions may have persisted at Boomplaas until approximately 6 000 BP when the most xeric conditions of the Holocene were experienced. There was "probably little or no rain in the warmer months with long, dry, hot summers." Although drier conditions prevailed, Scholtz (1986) recorded thicket taxa at 6 000 BP.

Since 6 000 BP, climatic conditions in the study area have probably been very similar to those experienced at present, with oscillations in wet and dry conditions. Tyson (1986) can find no evidence for progressive desiccation continuing to occur in southern Africa. The results of Meadows & Meadows (1988) confirms this for the study area.

Vegetation history in the Camdebo and Sneeuberg Regions: a qualitative model

The Grasslands and Shrublands

The Grasslands and Shrublands of the rocky slopes display the expected affinity with the Grassland and Savanna Biomes. During the period around 12 500 BP, the Winterberg palynological data shows high visibility of *Elytropappus* and Asteraceae, suggesting drier conditions (Meadows & Meadows, 1988). During these conditions the woody shrubs would probably have been restricted to the most mesic sites. The Shrubland would only have extended its range when conditions ameliorated, hence the low number of endemics in these communities(Table 3).

Table 3. An analysis of the flora of the Camdebo and Sneeuberg regions.

TOTAL FLORA

	KNR (Palmer, 1988b)	MZNP (Grobler, undated)	W/beeskuil (Hobson, 1984)	PRECIS	Estimated total	Total Nama-Karoo Flora (Gibbs Russell 1987)
No. species	338	499	179	418	1156	2147
% of total Karoo-Nama flora					53.8	

ENDEMICS

	KNR (Palmer, 1988b)	MZNP (Grobler, undated)	W/beeskuil (Hobson, 1984)	PRECIS	Total in 3224 Graaff-Reinet	Total 'unique' Nama-Karoo species (Gibbs Russell 1987)
Community						
Dwarf Shrublands	11	6	10	14	25	
Succulent Dwarf Shrublands	4		4	10	15	
Shrublands	2	3		4	6	
Grasslands		1		2	1	
Succulent Thicket	4		3	2	7	
No. endemics	21	10	17	32	54	377

KNR = Karoo Nature Reserve; MZNP = Mountain Zebra National Park.

The analysis suggests a remarkable similarity in the distribution patterns of the C4 species. *Heteropogon contortus, Digitaria eriantha, Cymbopogon plurinodis, Themeda triandra* and *Sporobolus fimbriatus* show similar proportions of their distribution in the Grassland Biome (26-33%) and in the Savanna Biome (38-46%). This corresponds with the suggestion that these grasses are associated closely with the woody shrubs of the savanna. The virtual absence of these species from the semi-arid pediments of the Nama-Karoo may be more a consequence of this association rather than increased aridity.

Species Group 5 is transitional between the mesic Shrublands/Grasslands and the Nama-Karoo elements. As more xeric conditions are being encountered in the phytosociological classification, a flora with affinity for to the semi-arid region occurs. This group, together with the abundant species such as *Pentzia incana*, is differential for the Dwarf Shrubland.

The Subtropical Thicket

Bearing in mind the results of studies of the Succulent Thicket (Palmer, 1981; Everard, 1987; Palmer *et al.*, 1988), I support the hypothesis (Cowling, 1983, 1986) that this vegetation was more extensive during warmer, wetter periods after 18 000 BP. Any Subtropical Thicket which may have occupied the region prior to this date would have been largely displaced during the LGM and would only have become established on edaphically favourable sites in the ameliorating conditions of the warmer, wetter Holocene. A low number of endemics (Table 3) suggests that this vegetation is a recent colonizer of these areas (Cowling, 1986).

In the 40 000 years preceding the LGM, the climate did not lend itself to the colonization of the area by woody shrubs and trees. During this period, it is possible that the arid corridor between the northeast (Saharo-Arabian) and the southwest areas of Africa may have existed (Verdcourt, 1969; van Zinderen Bakker, 1975; Raven & Axelrod, 1978) enabling the expansion of the desert flora, particularly the genera *Aristida, Cenchrus, Chenopodium, Cotula, Enneapogon, Euphorbia, Hibiscus, Indigofera, Tribulus* and *Zygophyllum* (Shmida, 1985).

The Dwarf Shrublands and Succulent Dwarf Shrublands

The Dwarf Shrubland and Succulent Dwarf Shrubland have a floristic integrity related to a long history in the region, with communities occurring under arid conditions, accompanied by soils with high base and fertility status. The Dwarf Shrublands may have been more extensive during the drier glacial times on those sites currently occupied by Grassy Shrubland and Grassland. It is suggested that during cool, dry conditions, "the Karoo complex probably moved further northward to an area where neither cyclonic rains nor tropical summer rains could affect it" (van Zinderen Bakker, 1978). Shmida (1985) states that although a land bridge may have existed in the Pleistocene, there are only eight true desert species shared between the Sahara and the Namib. Some well represented families in the study area (Aizoaceae, Amaryllidaceae, Crassulaceae and Iridaceae) are very poorly represented in the Sahara (Shmida, 1985). It is suggested that southern Africa was an ecological island, separated from the Sahara and Sahel (Shmida, 1985).

I suggest that the Dwarf Shrubland has been restricted to the pediplains of the region since long before the LGM, probably starting around 130 000 BP. Some evidence for this comes from the levels of endemism in the Dwarf Shrublands of the study area, with 25 of the 54 endemic species being recorded in these communities (Table 3). The extent of the Succulent Dwarf Shrubland, because of susceptibility to sub-zero temperatures, would probably have reduced at the time of the LGM.

The wet conditions after the LGM and up to 12 500 BP would have encouraged the development of a Grassy Dwarf Shrubland on the pediments. Axelrod & Raven (1978) suggest that the sclerophyllous vegetation of the Fynbos would have "invaded the present Karoo" during moist phases in the Pleistocene. The eutrophic soils of the Karoo pediments and bottomlands (Palmer, 1988c) are considerably different from the dystrophic soils in which Fynbos vegetation is encountered, and I suggest that the sclerophyllous vegetation would not have been successful. The high mineral levels in these soils, particularly Ca, would have favoured the development of Grasslands during wetter interludes. I support the suggestion of Cowling (1983) that the Fynbos has been largely restricted to the "edaphic island comprising the mountains of the Cape Fold Belt and that the flora was never displaced from this region". Although the Succulent Karoo flora displays greater affinity with the Fynbos, the same cannot be said for the Nama-Karoo. Species with Succulent Karoo Biome affinity are poorly represented.

Palynological data from Meadows *et al.* (1987) and Meadows & Meadows (1988) suggest that grasses replaced sedges in the mountain sites adjacent to the present Nama-Karoo during a drier period around 12 500 BP. This event would have led to desiccation of the pediments and a possible increase in the presence of dwarf shrubs and succulents dwarf shrubs. This would be akin to the conditions prevailing at present.

Concluding remarks

This qualitative model of vegetation history in the region provides additional testable hypotheses. Further evidence must be sort from the palaeosols to corroborate the age of the pediments and the nature, duration and timing of fluvial events. The evidence for the extent and composition of the pediment Dwarf Shrublands remains inconclusive and these elements of the model need further testing.

The preparation of the biome map should be viewed within the limitations it imposes on the conceptual understanding of the vegetation. The boundaries of the biomes, as presented by Rutherford & Westfall (1986), complement our understanding of the vegetation history of the Camdebo and Sneeuberg regions. The broad definition of the Savanna Biome by Rutherford & Westfall (1986) incorporates the Subtropical Thicket of the eastern coastal region (Everard, 1987; Lubke *et al.* 1988). I believe there is some justification for regarding this regional vegetation as a separate unit on the basis of structural differences.

The subtropical affinity of the Succulent Thicket is in contrast to the suggestion that Succulent Mountain Veld (Veld Type 25) is a karroid vegetation type (Acocks, 1975). More judicious agricultural treatment should be applied to this vegetation, bearing in mind that it is able to survive in an arid environment by virtue of the modifying effect which it has on the landscape. This is achieved in the creation of clumps of vegetation in which moisture is conserved (Palmer *et al.* 1988), modifying the plant/soil environment in relation to the adjacent Dwarf Shrubland. The abundance of CAM species (*Portulacaria afra, Crassula ovata* and *Aloe ferox*) may be a consequence of the success of these species when low night temperatures are experienced, as dark CO_2 fixation is enhanced by low night temperatures (Kluge & Ting, 1979).

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PART II

The reliability of using Landsat products to detect and map the vegetation of the region is assessed. The manual classification of Landsat standard products provides a poor reflection of the vegetation of the arid, sparsely-vegetated bottomlands and pediments. The products provide good representation of the boundaries of thicket vegetation, but this uni-temporal approach does not distinguish between floristically different thicket communities. After analyzing digital Landsat data, I suggest that the multi-spectral scanner detects the boundaries of broad soil pedons and geological formations in areas of low vegetative cover.

I describe and map the vegetation categories of the region after manual interpretation of six Landsat scenes. This is an efficient, cost-effective method of mapping vegetation in extensive regions. These mapping units do not adequately reflect the syntaxonomic classification arrived at earlier in the thesis, and represent an integration of physiographic, pedological, geological and floristic information. With the view to improving the classification of these units, I develop a qualitative model of the region using an expert system.

Using Landsat MSS data to detect and map vegetation units in the semi-arid Karoo region, South Africa: an assessment.

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ABSTRACT

Using the results of manual interpretation and digital data analysis, an assessment is made of the reliability of using standard Landsat MSS data to map the extent of natural plant communities in the semi-arid Karoo region of South Africa. The manual technique makes use of standard, edge-enhanced three-band colour composites. The standard products were used to map an area of ±20 000 km^2 between 32° and 33° S and 24° and 26° E. The map was prepared using a manual classification procedure, whereupon the result was compared with ground reference information. There was poor relationship between the classified map and the natural vegetation on the ground. This could be accounted for by the low vegetative cover of the pediments and bottomlands of the study area, and the floristic differences between structurally synonymous thicket vegetation.

In the digital assessment, MSS data from twelve sampling units on the Karoo Nature Reserve were used to prepare histograms of spectral response (Curran, 1983) patterns in all four Landsat bands. The results indicate that replicates within each sampling unit showed a significant relationship with one another, but between sampling units differences were great. The digital data suggest that the multispectral scanner on Landsat is detecting the boundaries of broad soil pedons and geological formations in areas of low vegetative cover.

Introduction

The efficient discrimination of vegetation pattern is an integral part of the application of remote sensing techniques to agriculture and land-use planning. In extensive, semi-arid regions of the world, land-use practices are resulting in transformation of the natural vegetation and soil erosion (Coiner, 1980). Acocks (1964), Roux *et al.* (1981) and Roux & Theron (1987) suggest that the semi-arid vegetation of the Karoo region of South Africa is expanding. With the knowledge that Landsat MSS data may be used to assess the relative change in surficial character of semi-arid environments (Frank, 1984a; 1984b), this desertification should be monitored. The remotely sensed data available in South Africa should be assessed for mapping and monitoring the extent and distribution of natural plant communities in this region. Earlier efforts to evaluate ERTS products (Jarman & Bosch 1973) and aerial photographs (Jarman, 1977) suggest that the products may be useful in monitoring the encroachment of karoo vegetation into the grasslands. Evaluation of satellite borne digital data from semi-arid regions in the northern hemisphere (Hielkema, 1979; McGraw & Tueller, 1983) suggests that misclassification of pixels is common in sites where vegetation is sparse. McCoy & Witt (1978) show that vegetation maps based on Landsat data become extremely unreliable when the vegetation cover is <20 %. The eastern part of the Karoo region contains a heterogeneous vegetation, with both sparsely (<20% cover) and densely (100 % cover) vegetated land parcels in close proximity to one another. The available remote sensing products would have to be assessed before a predictive model for mapping or monitoring vegetation could be prepared.

The karoo biome has become the focus of research attention in southern Africa since the initiation of the Karoo Biome Programme in 1984 (Cowling, 1987). The eastern section of the Karoo lies in a floristically complex area where the vegetation from five phytochoria meet (Palmer, 1988a). Examples of vegetation from the Savanna, Nama-Karoo, Grassland, Fynbos and Forest Biomes (Rutherford & Westfall, 1986) are encountered in the study area. Being a tension zone between these phytochoria makes the study area an ideal outdoor laboratory for developing and testing hypotheses on the changes in the distribution of components of the flora. The first step in this process is to prepare an accurate inventory of the plant communities encountered using an objective mapping technique.

The study area

The study area (Fig. 1) extends from 32° S to 33° S latitude and 24° E to 26° E longitude, corresponding with the 1:250 000 S.A. Topo Series sheet 3224 Graaff-Reinet. The structure of the natural vegetation varies from the semi-arid, Succulent Dwarf Shrubland to the mesic, Afro-

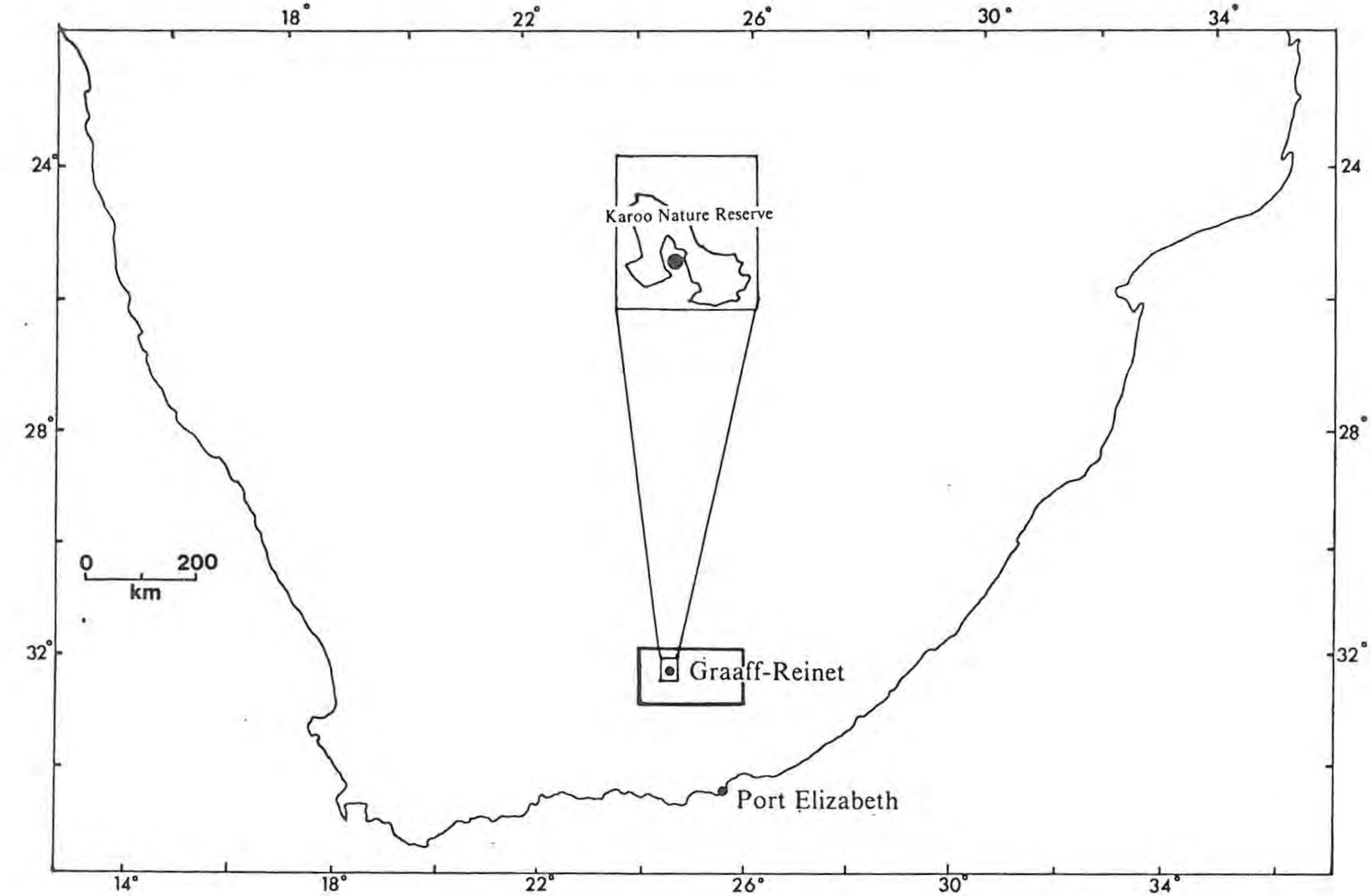

Fig. 1. The location of 1:250 000 S.A. Topo Series Sheet 3224 Graaff-Reinet and the Karoo Nature Reserve.

montane Forest and Grassland over an extremely short distance (50km), and a steep precipitation gradient is the principal environmental variable. Mean annual rainfall varies from <250 mm in the south west to >600 mm on the mountains in the south east.

The vegetation of this section of the karoo biome has received little syntaxonomic treatment, although numerous researchers have carried out parochial studies in the region (Werger 1980, Jooste 1980, van der Walt 1980, Palmer 1988b). Acocks' (1975) treatment of the vegetation has had to suffice as an overall vegetation classification of the biome. Within 3224 Graaff-Reinet, Acocks (1975) recognized thirteen Veld Types. This is a reasonably large number of units (probably equivalent to order) and the classification cannot be regarded as inadequate, although the relationships between vegetation units require further refinement.

Methods

Manual Interpretation

A pre-requisite to any mapping programme using remotely sensed data is that reliable ground reference information be collected at the time the remotely sensed data is recorded (Smedes, 1975). The Satellite Remote Sensing Centre (SRSC) started receiving and processing Landsat-2 imagery in December 1980 (Botha, 1982), and I initiated the collecting of total floristic information in the region while undertaking semi-detailed vegetation studies on small nature reserves. This programme was extended to collecting total floristic information in all relatively uniform vegetation-soil systems in the region. The nature reserves served as a training site for the development of vegetation concepts from which the regional extrapolations were to be made. Stratification of imagery into Landsat Sampling Units (LSU)(Cihlar & Thompson, 1978) is the first step in employing Landsat MSS data to map large sections of a regional flora (McDaniel & Haas, 1980; Jarman & Jackson, 1981).

The SRSC offers a range of standard products to the user community (Botha, 1982). A different procedure may be used to prepare each product, and the preparation has a direct bearing on its value to the end-user. The satellite-borne multi-spectral scanner (MSS) is capable of recording radiance from the earth's surface in four spectral bands: 500-600; 600-700; 700-800 and 800-1100 nm, usually referred to in the case of Landsat-2, -3 & -4 as MSS4, MSS5, MSS6 and MSS7. These data are recorded as a binary number for each of the approximately 2,5 million pixels (picture elements) in a standard Landsat scene (Westfall & Malan, 1986). Once received and recorded by the SRSC, they can be processed in a number of ways. The most common process is to create a master negative at a scale of 1:1 million. The master is produced by subjecting each pixel in three bands (MSS4, MSS5 and MSS7) to a simple summation algorithm (Marais, pers. comm.). The product is then converted to film format by an electron beam recorder (White, 1977). This is in effect an artist's impression of the data, as the amount of "redness" or "blueness" can be manipulated to suit the composer. This is termed a "false colour composite" with MSS4, MSS5 and MSS7 displayed respectively as the colour primaries blue, green and red.

The image generated in this manner provides the user community with a relatively in-expensive product which represents an acceptable summary of the digital data, albeit statistically changed. The SRSC provides two types of standard products (Botha, 1982) from this master negative:
i) 1:1 million three-band colour composite positive film transparencies;
ii) 1:250 000 colour composite prints.

Five Landsat-2 scenes and one Landsat-4 scene were required for coverage of the 3224 Graaff-Reinet (Table 1). Although Mack *et al.* (1984) report that extrapolations of the data from one system to another are not advisable in vegetation analysis, I elected to use the Landsat-4 scene to complete a small area of the rectangle. In view of the expense involved in acquiring imagery, it was decided to select those wet-season scenes providing cloud-free coverage of the study area. As vegetation structure and cover were the most important attributes being mapped, summer scenes provide greatest contrast. During the selection process I found that winter scenes for the study area showed a lack of differentiation between known vegetation units.

Only limited coverage of colour prints at 1:250 000 could be obtained within the budget constraints of the project. Suitable methods for presenting the information contained on the 1:1 million positives at the semi-detailed (1:50 000) and reconnaissance (1:250 000) scales were developed. Firstly, the 1:1 million positive was enlarged on a micro-Fiche reader (Palmer, 1982). This provided a useful enlargement of the image, but the scale remained constant at ±1:45 000. In addition, the size of the positive transparency made it difficult to enlarge all parts of the image on the micro-Fiche reader. "Eye-balling" was possible when the transparency was placed on a overhead projector (Harrington & Dunn 1980), but a loss of quality on enlargement detracted from this method.

The most successful option has been the copying of portions of any scene with commercially available transparency film through a 55mm Macro lens with a natural light source (Harrington & Dunn, 1980). The copy was then projected onto a sandblasted glass screen and adjusted to the fit an acetate copy of the applicable 1:250 000 Topo Series Sheet, obtainable from the Director-General, Surveys & Mapping. The image was registered with 3224 Graaff-Reinet by means of known land marks i.e. airfields, road intersections, towns; and where none of the

Table 1. Details of the 6 Landsat scenes used to identify Landsat Sampling Units on 1:250 000 Topo Series Sheet 3224 Graaff-Reinet.

WRS	Scene ID	Date	Area description, scale and type of product
171-83	41138-07335	27/8/1985	Jansenville, Somerset-East 1:1 mil. systematically corrected, edge-enhanced 3-band colour composite
183-82	22332-07232	11/6/1981	Cradock 1:1 mil. systematically corrected, edge-enhanced 3-band colour composite
183-83	22314-07241	24/5/1981	Jansenville 1:1 mil. systematically corrected, edge-enhanced 3-band colour composite
184-82	22117-07312	8/11/1980	Graaff-Reinet 1:1 mil. systematically corrected edge-enhanced 3-band colour composite. Test image
184-82	22477-07282	3/11/1981	Graaff-Reinet 1:250 000 systematically corrected, edge-enhanced 3-band colour composite
184-83	22477-07284	3/11/1981	Aberdeen 1:1 mil. systematically corrected, edge-enhanced 3-band colour composite

above were in the vicinity, rivers and mountain ranges. Registration in this manner was crude and is only recommended for reconnaissance scale surveys.

Based on tone and texture, the boundaries of each relatively homogeneous LSU were drawn. The entire image was scanned for related patterns. When a new image was being interpretted, an area which had already been completed was matched with the new image. This enabled the observer to train her eye to the new image. The process was repeated for each of the six scenes required to provide complete coverage of 3224 Graaff-Reinet. Each LSU was classified into one of twenty initial spectral response classes (SRC's).

The SRC's on the completed 1:250 000 sheet were colour-coded using Windsors & Newtons Town and Country Planning Colours and each LSU was allocated a unique reference number. This product was used as the stratified map for the selection of sampling sites for the regional vegetation survey using the methods of the Zürich-Montpellier school of phytosociology (Palmer, 1988c). A vegetation bench-mark site for each SRC was established in the training area (Karoo Nature Reserve) using the classification developed by Palmer (1988b) and these were regarded as the cover classes (CC's) for that SRC. By means of subjective assessment, the floristic and structural attributes of the vegetation of each LSU were compared with the vegetation of the bench-mark sites for that cover class. If the vegetation of the LSU did not correspond with the bench-mark, it was compared with other bench-mark sites until agreement was reached amongst the observers. In the event of the existing bench-mark sites not providing the necessary similarity, a new cover class was created.

Digital Interpretation

In the Karoo Nature Reserve, Graaff-Reinet, the steep precipitation gradient has encouraged the development of diverse vegetation types. As the vegetation of this area was representative of much of the regional flora, I selected it as a training area and examined the digital data recorded by Landsat-2. The objective was to provide a measure of statistical validity to the manual interpretation procedure.

Based on tone and texture, twelve sampling units (Table 2) were identified using the manual technique described by Palmer (1982). A map of the boundaries of these units was prepared and sent to the SRSC for further interpretation. The image ID 22117-07312: WRS 184-82 of 8 November 1980 was the first frame of WRS 184-82 received by the SRSC and contained bad data points (Boyle, pers. comm.). The whole image was dehazed and sun angle normalized to 60°. The haze bias for each band was 12, 18, 18, and 5 for MSS4, MSS5, MSS6 and MSS7

Table 2. Sampling units distinguished during the digital assessment of land cover around the town of Graaff-Reinet.

Sampling unit	Colour	Vegetation type/Land cover	Soil colour (Munsell)	Cover Class
1	light grey	succulent dwarf shrubland	7.5YR4/4	8
2	grey	dwarf shrubland	7.5YR5/6	9
3	light red and blue	mesic grassland and thicket	n/a	6
4	light red	mesic deciduous thicket	n/a	6
5	white	degraded dwarf shrubland	5YR5/5	6
6	dark blue	shallow water and mud	n/a	n/a
7	light red	shrubland	10YR3/2	1
8	dark red	succulent thicket	10YR5/4	13
9	pink and blue	urban	n/a	n/a
10	clear	succulent dwarf shrubland	7.5YR5/4	8
11	clear brown	open succulent thicket	10YR5/4	13
12	light brown	shrubland	10YR3/2	1

n/a = not available

respectively. The actual sun angle was 51,19°.

Replicates were selected within each of the sampling units by the image analyst at the SRSC without local knowledge. The approximate location of each replicate is indicated on Figure 2. Only rectangular sites were chosen, and the numbers of pixels per replicate varied (Table 3). The number of times each binary value was recorded in each replicate was determined. Where bad data spots were encountered these were removed from the data and the relative proportions of the contribution of each binary number calculated. The mean pixel value within each band for each sampling unit was calculated, together with the standard deviation.

Results

Manual Interpretation

Twenty SRC's and two hundred and twenty seven LSU's were initially identified in 3224 Graaff-Reinet. The SRC's were finally reduced to twelve cover classes after the reconnaissance survey, and a full vegetation description for each is given by Palmer (1988) and summarized in Table 4. One hundred and forty-nine LSU's were visited. The initial SRC numbers have been retained to avoid confusion, hence the absence of cover classes 5,7,10,11,12,15,16,17 and 19.

With the SRC regarded as the predicted cover class, an extremely poor relationship exists between predicted and recorded cover class (Table 5). Only 49,6 % of LSU's remained in their predicted cover class. The class showing the most reliable predictability is Succulent Thicket (CC 13). The vegetation in this class contains a high proportion of succulent and woody shrubs. These parcels occur in easily distinguishable, isolated stands. It was only possible to differentiate these stands from the forest and woody riparian thicket by association and observer knowledge.

The second most predictable class was the sparse vegetation associated with the duplex, alluvial soils of the bottomlands (CC 4). This is most likely a consequence of the high reflectance attributes of these sites. The shrubland in which *Acacia karroo* occupies sites on mountainous terrain (CC 14) is also moderately predictable (75%). The least predictable cover type was the extensive grassland and shrubland associated with the rocky, mountainous terrain (CC 1).

Digital interpretation

The spectral response curves (McCoy, 1981) for the sampling units in and adjacent to the Karoo Nature Reserve are presented in Figs. 3-6. The sampling unit numbers are specific for this aspect of the project and do not correspond with those used in the manual interpretation, with

Table 3. Details of the numbers of replicates, numbers of pixels and standard deviation of the eleven sampling units identified around Graaff-Reinet.

Sampling unit	No. of replicates (n)	Mean No. of pixels/replicate $\bar{x}$	sd
1	7	262,3	173,1
2	9	249,2	100,9
3	3	400	13.06
4	3	120	73.3
5	2	160	20
6	2	242	34
7	8	336	129
8	5	130	30.2
10	3	268	48.1
11	3	451	185.8
12	4	228	129.5

LEGEND

———————	Roads
2/	Landsat Cover Class
/3	Replicate within each class
〰〰〰	Boundaries of homogeneous units

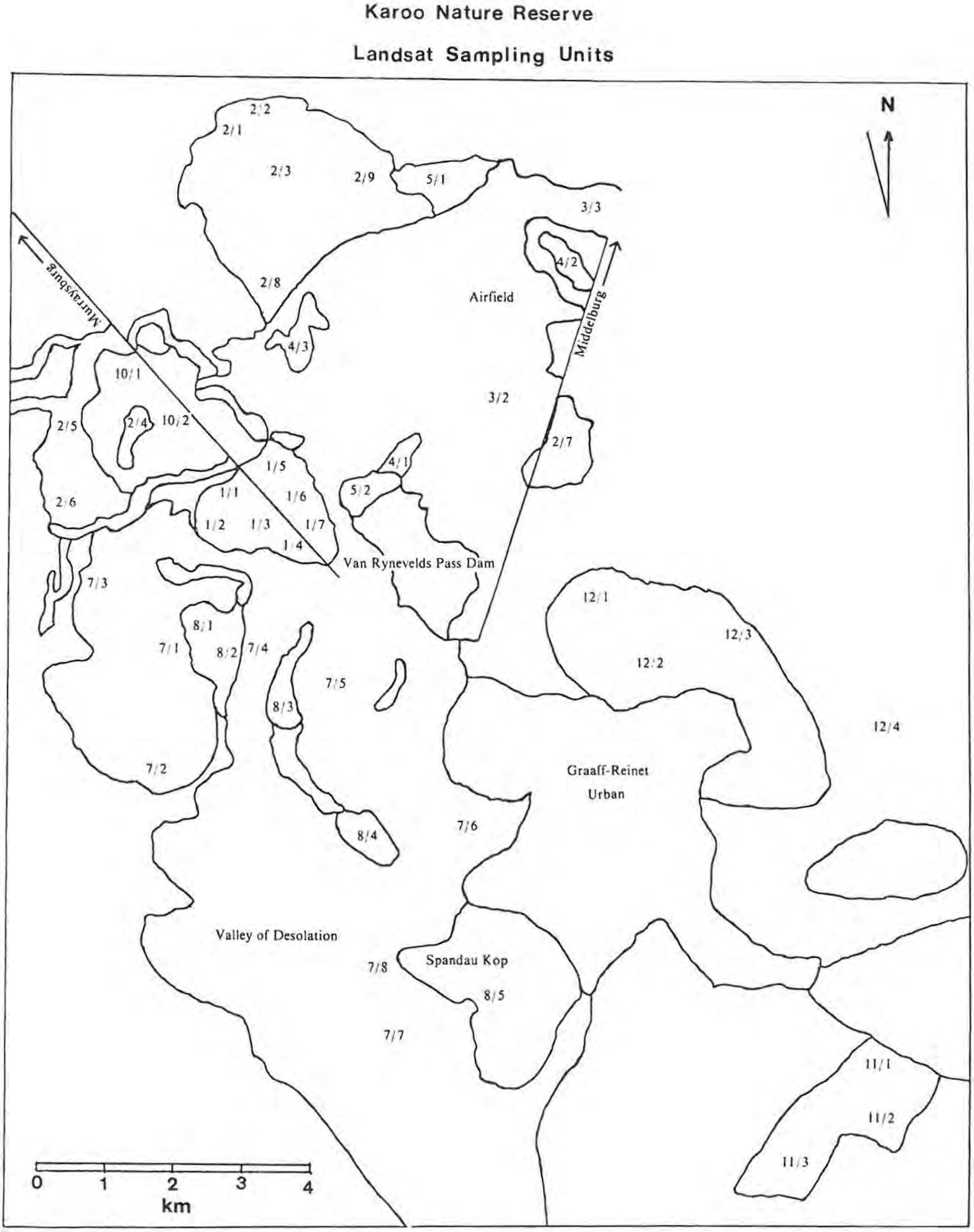

Fig. 2. Sampling units on and adjacent to the Karoo Nature Reserve, showing the approximate location of replicates within each unit.

Table 4. The twelve cover classes identified on 3224 Graaff-Reinet using the manual interpretation procedure.

Cover Class	Vegetation type (Palmer 1988e)	Dominant geology
1	Montane shrubland and grassland	Dolerite
2	Grassy dwarf shrubland on footslopes	S/stone & dolerite
3	Grassy dwarf shrubland on dolerite plateaux	Dolerite
4	Degraded dwarf shrubland on alluvium	Alluvium
6	Riparian thicket	Alluvium
8	Succulent dwarf shrubland on pediments	Alluvium
9	Dwarf shrubland and grassy dwarf shrubland on pediments	Sandstone
13	Succulent and non-succulent thicket	Dolerite & mudstone
14	Thorny shrubland on rocky slopes	Sandstone
18	Grassy open shrubland on sandstone	Sandstone
19	Grassland	Sandstone
20	Afro-montane Forest	Sandstone

Table 5. A summary of the classified and misclassified LSU's in the important cover classes, showing the percentages of each class changed during the field assessment. The percentage of correctly classified LSU's in each cover class are highlighted. The numbers in brackets are the number the sample size.

SRC or predicted cover class	Recorded cover class	% total number of LSU's in the predicted class	% misclassified LSU's
1	1 (6)	**25**	
1	3 (1)	4.2	
1	13 (8)	33.3	
1	14 (9)	37.5	75
2	2 (4)	**36.4**	
2	6 (1)	9.1	
2	9 (3)	27.2	
2	13 (2)	18.2	
2	19 (1)	9.1	63.6
3	1 (1)	5.9	
3	3 (9)	**53.0**	
3	8 (3)	17.6	
3	9 (3)	17.6	
3	14 (1)	5.9	47.0
4	4 (11)	**78.6**	
4	8 (1)	7.1	
4	9 (2)	14.3	21.4
5	8 (4)	80	
5	9 (1)	20	100
6	1 (1)	-	-
7	1 (4)	57.1	
7	3 (1)	14.3	
7	9 (1)	14.3	
7	13 (1)	14.3	100
8	8 (9)	**60**	
8	9d (3)	20	
8	9 (3)	20	40
9	9 (8)	**57.2**	
9	9d (3)	21.4	
9	14 (3)	21.4	42.8
11	1 (1)	20	
11	4 (3)	60	
11	13 (1)	20	100
12	3 (2)	-	
13	1 (2)	11.8	
13	13 (14)	**82.3**	
13	20 (1)	5.9	17.7
14	9 (3)	18.7	
14	9d (1)	6.3	
14	14 (12)	**75.0**	25.0
18	18 (1)	0	-

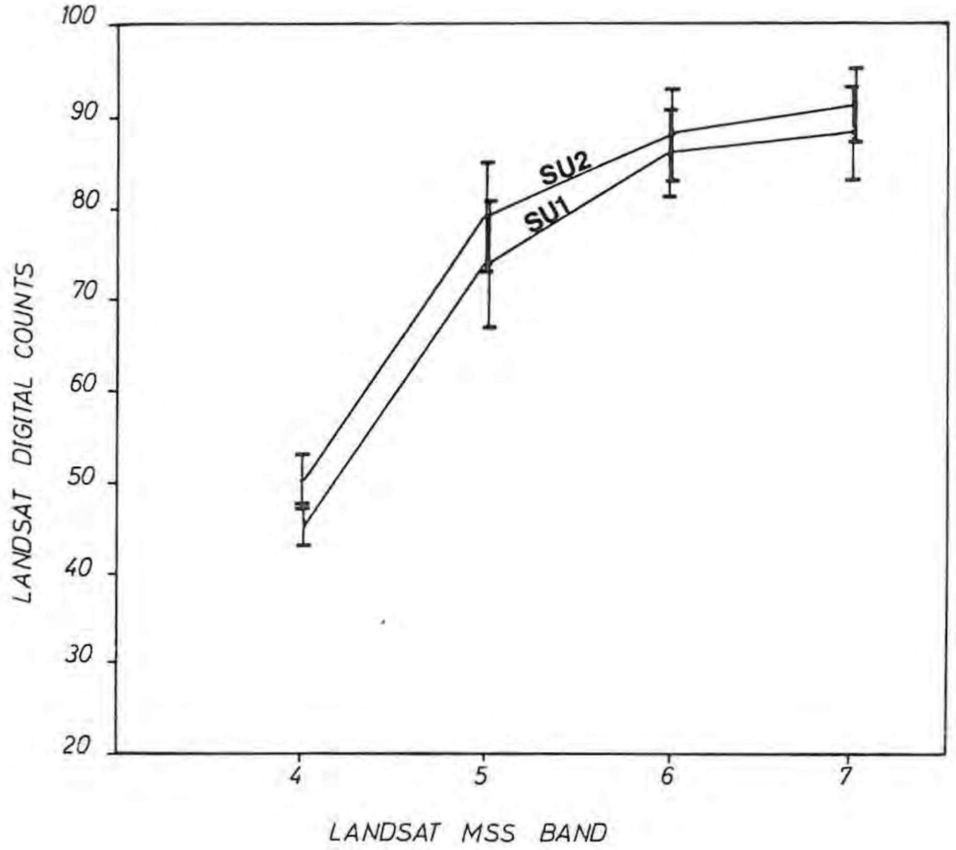

Fig. 3. Spectral response curves for sampling units (SU's) 1 and 2.

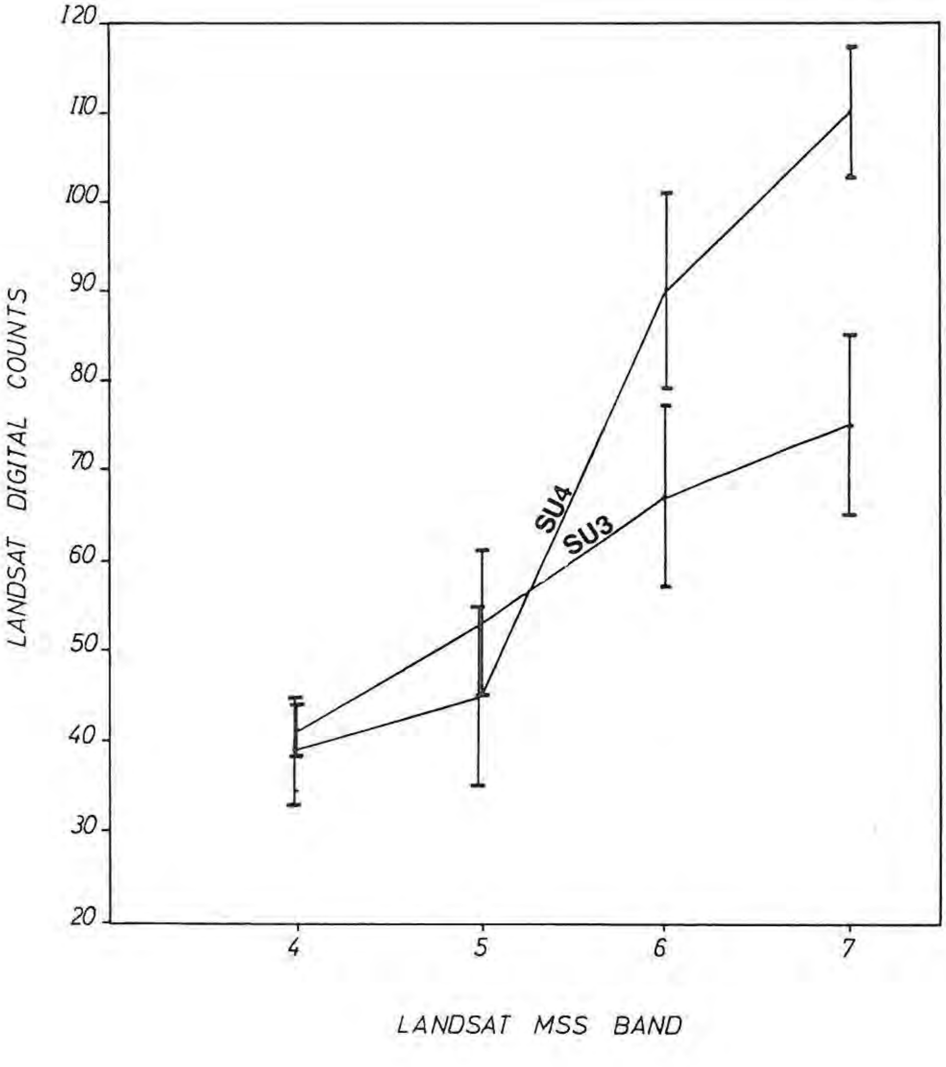

Fig. 4. Spectral response curves for sampling units 3 and 4.

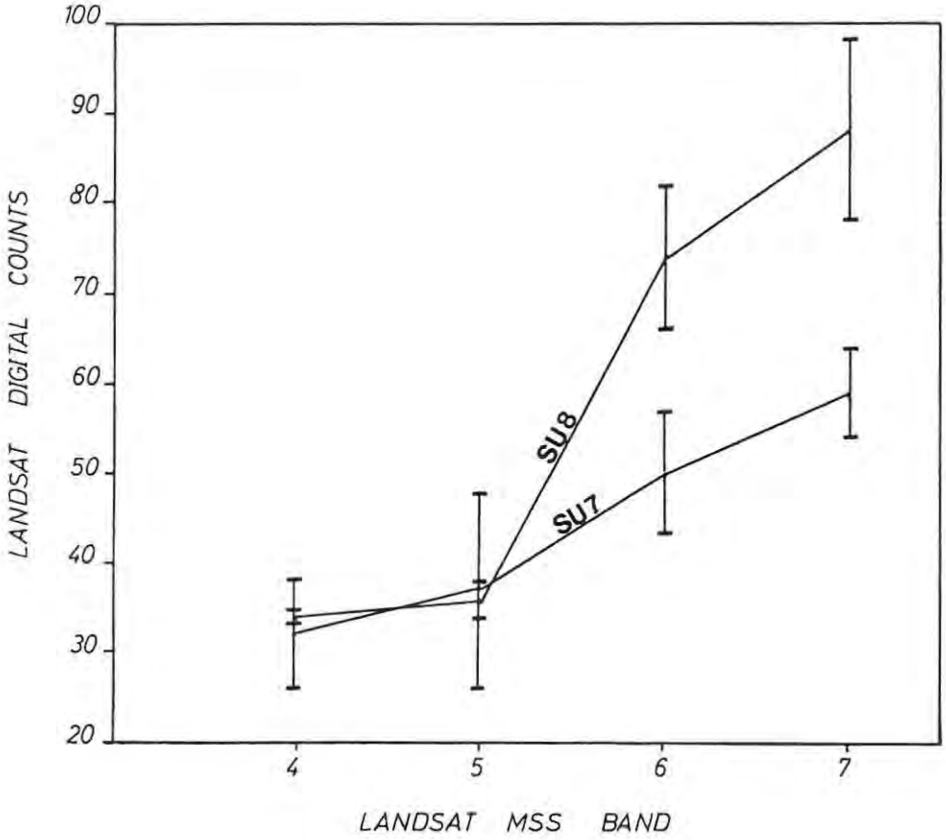

Fig. 5. Spectral response curves for sampling units 7 and 8.

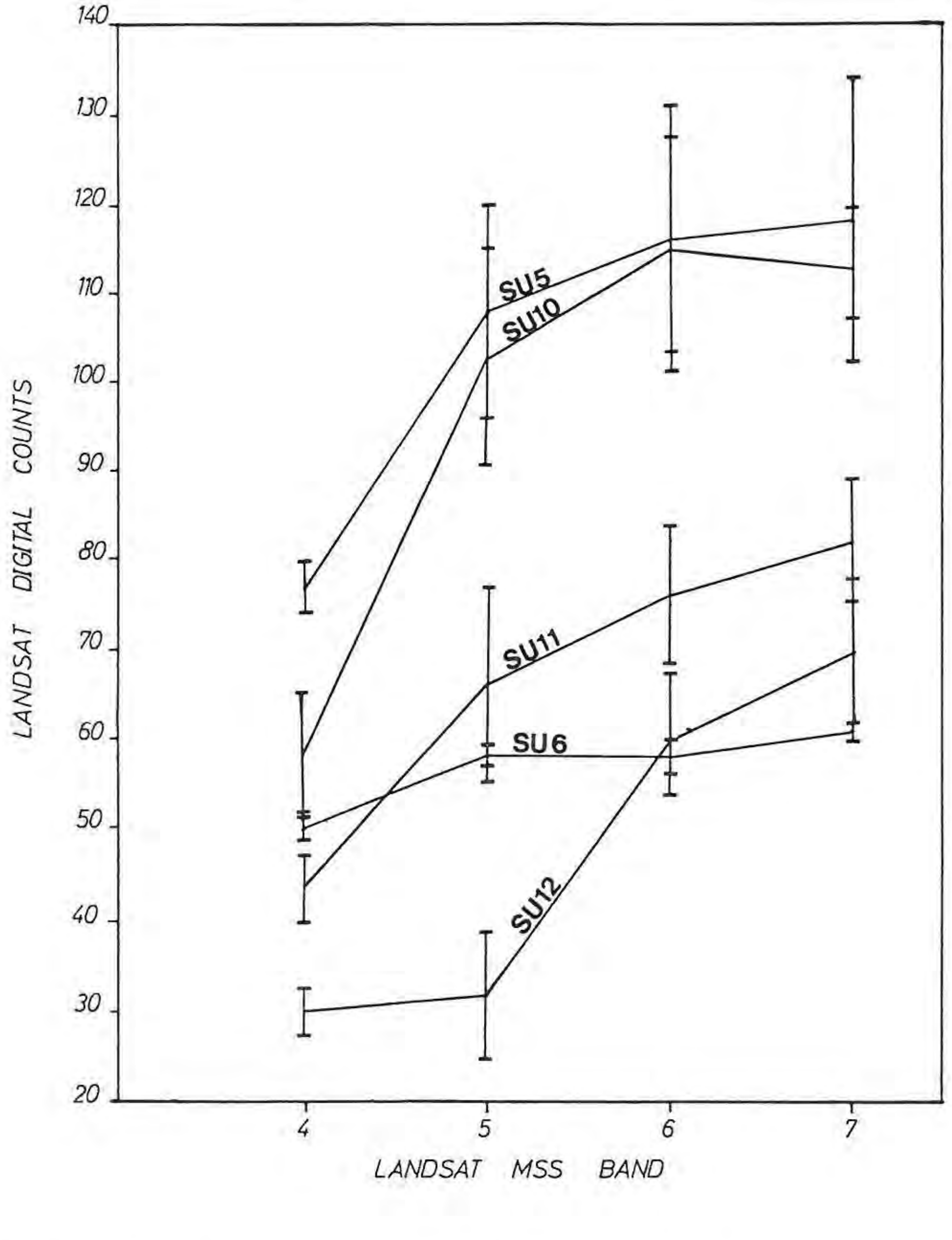

Fig. 6. Spectral response curves for sampling units 5, 6, 10, 11 and 12.

the comparative classes presented in Table 3. Certain spectral response patterns were found to be too specific and limited in their distribution e.g. urban (sampling unit 9) and shallow water and mud (sampling unit 6). No further analysis was undertaken on the former sampling unit (Table 2), whereas the latter was analysed further as it contained examples of natural perennial grass cover.

Using the digital data it was not possible to distinguish between floristically disparate plant communities on the pediment and foot slopes where low total cover values were being experienced. The Dwarf Shrubland of the pediment was not distinguishable from the Succulent Dwarf Shrubland the rocky footslope (Fig. 3). Similarly in areas of high cover the Landsat digital counts for *Portulacaria afra* dominated succulent thicket (Fig. 4) were not significantly different from the *Acacia karroo* - dominated riparian thicket (Fig. 5).

There remains a clear distinction between the disturbed *Cynodon dactylon* grassland, (Fig. 6) the dwarf shrublands (Fig. 3) and the thickets (Figs. 4 & 5). This may be an anomaly of the soil moisture and soil background effects in each case.

Discussion and recommendations

Manual interpretation of uni-temporal Landsat MSS data does not provide a reliable model for predicting and mapping the plant communities of the Karoo. Todd, Gehring & Haman (1980) report in an assessment of wildland mapping accuracy that "classification error is directly related to trying to extract Landsat-derived resource classes whose spectral characteristics approach - and sometimes reach - the noise level of the data". It is likely that the multi-variate nature of the natural land cover in the Karoo region precludes the possibility of successfully providing low noise data. This noise detracts from the effectiveness of the human eye in discerning homogeneous spectral response classes. Quirk & Scarpace (1982) report similar results when comparing the accuracy of land-cover estimates using manual interpretation of aerial photographs and computer analysis of Landsat MSS data. Manual interpretation of colour infrared photographs provided less accurate land-cover estimates than Landsat.

The results of the digital assessment, particularly the lack of difference between sampling units 6 and 8, support the findings of Gausman *et al.* (1978), who report that it is not possible to distinguish between succulent and woody thicket in a single scene. In the semi-arid regions, the separation of vegetation types is caused by soil background, topography and vegetation vigour (Salmon-Dresler, 1977). This is supported by the findings of this study.

Comparison of the spectral response curves in the Dwarf Shrublands and Succulent Dwarf Shrublands supports the findings of Westin & Lemme (1978), namely that soil influences all vegetative spectral response to some degree. In common with the experience of Ezra *et al.* (1986), the Landsat digital count in areas of lower cover values increased with decreasing darkness of soil colour. The mean response curve of the succulent dwarf shrubland (Fig. 3) corresponds very closely with McCoy's (1981) class of $<15\%$ cover. Elvidge & Lyon (1985) report that variations in rock-soil brightness have a strong influence on the ratio-based vegetation indices. These ratio-based indices overestimate the vegetation on dark backgrounds and underestimate the vegetation on bright backgrounds. The results of this project show that vegetation on light yellow red soils (5YR5/5) had implied lower vegetative cover and lower mean pixel values than darker soils. No objective basis for this result could be found in the cover values from the phytosociological table where total cover seldom fell below 30%. These differences must be due to substrate features other than vegetative cover.

The MSS data provides the boundaries of sampling units, which may be used as a stratified map to select sites for the collection of data for a Natural Resource Inventory (NRI). In the sparsely vegetated pediments and bottomlands, these LSU's are probably more closely akin to the landforms described by Pain (1985) and modified by Palmer (1988d), than to vegetation. Each LSU may be further classified using information on additional attributes recorded on the NRI Worksheets with ECOCLASS (Palmer, 1988d), an interactive classification procedure.

Future research should be undertaken to ascertain which land cover attributes strongly influence spectral response patterns and to develop a multi-temporal model of the spectral response of sensitive sites in the semi-arid region. This could be undertaken as a earth-based study using a hand-held radiometer (Lemme & Westin 1979; Schreier *et al.*, 1982; Saint, 1987) and would represent an important contribution to the objective, repeatable, monitoring for large scale transformations of land cover due to anthropogenic influence. It would then be possible to prepare details of the most sensitive attributes to record at each inventory site.

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The mapping and description of the vegetation categories of the central area of the Cape midlands with accompanying 1:250 000 S.A. Topo Sheet 3224 Graaff-Reinet.

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Abstract

A scheme of categories for the vegetation in and adjacent to the Camdebo and Sneeuberg regions of the karoo biome is given as a second approximation after Acocks' Veld Types (1975). Thirteen categories or cover classes of vegetation are presented. The major divisions, recognized on the basis of their landform features, are the vegetation of: the bottomlands, pediments, footslopes, convex and concave slopes, plateaux and rocky ridges. The major sub-divisions recognized on the basis of structural and floristic attributes are: Succulent Dwarf Shrublands; Dwarf Shrublands; Grassy Dwarf Shrublands on the footslopes; Grassy Dwarf Shrublands on dolerite plateaux; Degraded Dwarf Shrublands; Montane Grasslands with shrubs and dwarf shrubs; Grassy Open Shrublands on sandstone; Riparian Thicket; Succulent Thicket; Noorsveld; and Grasslands. The floristic elements of these subdivisions show affinity with the following biogeographical regions: Karoo-Namib region; Tongaland-Pondoland Regional Mosaic; Sudano-Zambezian region; and Afro-montane region. A vegetation map on which these categories are recognized were produced using Landsat imagery.

Uittreksel

'n Uiteensetting van kategorieë van die plantegroei in en aangrensend aan die Camdebo- en Sneeuberg-streke van die karoobioom word gegee as 'n tweede benadering na Acocks (1975) se Veldtipes. Dertien kategoriee of bedekkingsklasse van die plantegroei word aangebied. Die vernaamste verdelings wat herkenbaar is op die basis van hulle landskap eienskappe is die plantegroei van: laagland; pediment; voorskoot; bol- en hol-hellings; plato's en rotsagtige rantjies. Die vernaamste onerverdelings wat herkenbaar is op die basis van hulle strukturele en floristiese kenmerke is: Bergagtige Grasveld met struike en dwerg struike; Dwergstruikveld van die voorskoot; Grasagtige Dwergstruikveld; Sukkulente Dwergstruikveld; Dwergstruikveld; Versteurde Dergstruikveld; Oewerruigte; Grasagtige Ope Struikeveld; Sukkulente Struikgewas; Grasveld. Die floristiese elemente van hierdie sub-divisies toon verwantskappe aan die volgende biogeografiese streke: Karoo-Namib streek; Tongaland-Pondoland streek; Sudano-Zambezian streek; en die Afro-montane streek. 'n Plantegroeikaart waarop hierdie kategorieë erken word, is opgestel met die gebruik van Landsatbeelde.

INTRODUCTION

Research programmes in southern Africa since 1979 (Jarman *et al.* 1981, Co-ordinator for Remote Sensing 1982, Jarman *et al.* 1983b) stimulated my interest in assessing the standard Landsat products. Vegetation reconnaissance in the Camdebo and Sneeuberg regions of the Nama-Karoo biome provided the opportunity to embark on the project (Palmer 1988a).

Information on the cover of the earth's surface has improved since the advent of satellite-borne multi-spectral scanners (MSS) and researchers have been encouraged to use these data for mapping natural features. The process of mapping must follow the rules of logic, since "violation of these rules can render the map incorrect, incomplete, inconsistent, or misleading" (Robinove 1981). "The essence of mapping is to delineate areas that are homogeneous or acceptably heterogeneous" (Varnes 1974). Mapping may be carried out in one of two ways:

i) an *a priori* classification scheme is generated for the feature which is being mapped; or

ii) an *a posteriori* classification scheme is arrived at after the units in a population have been analysed comprehensively using surrogate data.

In the former approach, the classification is selected without regard to the particular land area being classified. The scheme is difficult to develop and use but it does provide a consistent theoretical framework upon which different individuals can accumulate comparable results. The scheme must consider the total population of the attribute (both inside and outside the area under consideration) and must explicitly define the boundaries of each class in an unambiguous manner (Robinove 1981).

In the latter scheme, surrogate data may be used to infer the important attributes of the feature being mapped. The information collected in each unit is used to describe the unit and a hierarchical classification scheme may be developed to indicate interrelationships between units. This scheme may be based on all or part of the information collected about the unit. The scheme necessitates a greater amount of post-mapping field reference work, and requires that the nature of the information collected during the field work be carefully determined. The *a posteriori* map generated may be a reflection of an attribute which is not even recorded during the field reference work.

Both *a priori* and *a posteriori* classification procedures can be used to interpret satellite data. The latter is carried out when a supervised classification of satellite data is required based on information collected in a smaller training site. This has a number of disadvantages when dealing with vegetation mapping:

a) the "training site" will in all likelihood not be representative of the vegetation of the whole scene being classified.

b) expensive computer time is required to generate the "map" from the digital data. If any new attribute is then identified which cannot be accounted for by an *a priori* classification scheme adopted, a new map has to be generated with the new attribute included.

c) with vegetation mapping in southern Africa, the scale of 1:250 000 has been adopted following the Director-General, Surveys and Mapping. At this scale, many scenes may be required to adequately cover the area of the map. As these are often multi-temporal images, training sites would have to be located in each scene and a supervised classification carried out in each case. Once again this would be a costly, time-consuming exercise.

The *a priori* classification schemes have been used to map fynbos in southern Africa (Jarman *et al.* 1981). Jarman (pers. comm.) recommends that an *a posteriori* approach be applied in the case of reconnaissance survey, making use of Satellite Remote Sensing Centre (SRSC) standard products. Robinove (1981) supports the latter approach when using digital data. Landsat computer compatible tapes (CCT's) are a source of proxy vegetation data (Hicks 1977, Laperriere *et al.* 1980, Jarman *et al.* 1981). Hicks (1977) reports that five major vegetation categories can be differentiated with the aid of CCT's of Landsat MSS data and suggests that these products possess characteristics which warrant their continued evaluation in land resource inventory mapping.

Manual photo-interpretation techniques have been applied to standard Landsat false colour composites (FCC's)(Harrington & Dunn 1980). Examples of visual-manual data extraction techniques are described by Steiner & Salerno (1975). Jarman *et al.* (1983a) report that digital processing for vegetation mapping, with a final map scale of 1:1 000 000, did not exactly simulate the products obtained by visual interpretation. Digital processing of Landsat CCT's should at best be regarded as a tool in vegetation mapping, to be used in conjunction with visual interpretation. The literature is ambiguous about the reliability of using FCC's or CCT's to map natural vegetation on scales from 1:250 000 to 1:1 million.

I present a map of the vegetation of the Camdebo and Sneeuberg regions after interpretting Landsat imagery. The interpretation employs an *a posteriori* mapping scheme, in contrast to the intensive *a priori* approach. I present this approach with the view to evaluating the continued use of Landsat imagery to predict vegetation pattern in the relatively flat semi-arid areas of southern Africa.

MAPPING METHOD

Landsat imagery was purchased to cover the 1:250 000 Topo Series sheet 3224 Graaff-Reinet (Table 1). Two standard products (Botha 1982) were used: 1:250 000 paper positives of a three-band colour composite and 1:1 000 000 film positives of the systematically-corrected edge-enhanced three band colour composites. An acetate film basemap, containing standard topographical features, was obtained from the Director-General, Surveys and Mapping. This map was superimposed on the 1:250 000 paper positive and registered with visible landmarks. An overlay was prepared on Barker Hi-trans film.

The delineation of cover classes was based primarily on tonal differences within the study area. Textural differences were used to a lesser extent. The shadow effect was taken into account in areas of extremely rugged terrain, and the cover class of the areas in shadow was assumed to be the same as adjacent vegetation not in shadow. Pattern and association were important in delimiting the vegetation accompanying stream and river courses, and areas which had been cleared of natural vegetation.

The technique for 1:1 million FCC's was slightly different. A screen of sand-blasted glass was constructed onto which 35 mm colour transparencies of portions of each scene were projected. The copies of portions of the scene were made using a 35mm SLR camera and a 25-50 mm Macro lens, with a natural light source. There was relatively little loss of detail associated with the photographic process using this procedure, contrary to the opinion expressed by Harrington & Dunn (1980).

The 1:250 000 Topographical map and the Barker Hi-trans film were placed on the screen and the 35mm transparencies rear-projected. The screen was adjusted until registration with at least two reliable reference points was achieved. The delineation of all spectral response classes was undertaken on the basis of the tonal differences (Table 2). The observer ensured that an area common to the previous and current image appeared on the screen. This ensured eye-training before each part of the image was classified. The spectral response class was indicated in the delineated area and colour coded. Each relatively homogeneous unit was allocated an individual number and called a Landsat Sampling Unit (LSU) (Cihlar *et al.* 1978). Two hundred and twenty one LSU's were recognized on 3224 Graaff-Reinet.

Following Hicks (1977), I developed a Natural Resource Inventory Worksheet (NRIW). The recording system comprises proformas for floristic, structural, pedological, remote sensing,

Table 1. Details of the 6 Landsat scenes used to identify Landsat Sampling Units on 1:250 000 Topo Series Sheet 3224 Graaff-Reinet.

WRS	Scene ID	Date	Area description, scale and type of product
171-83	41138-07335	27/8/1985	Jansenville, Somerset-East 1:1 mil. systematically corrected, edge-enhanced 3-band colour composite
183-82	22332-07232	11/6/1981	Cradock 1:1 mil. systematically corrected, edge-enhanced 3-band colour composite
183-83	22314-07241	24/5/1981	Jansenville 1:1 mil. systematically corrected, edge-enhanced 3-band colour composite
184-82	22117-07312	8/11/1980	Graaff-Reinet 1:1 mil. systematically corrected edge-enhanced 3-band colour composite. Test image
184-82	22477-07282	3/11/1981	Graaff-Reinet 1:250 000 systematically corrected, edge-enhanced 3-band colour composite
184-83	22477-07284	3/11/1981	Aberdeen 1:1 mil. systematically corrected, edge-enhanced 3-band colour composite

Table 2. Sampling units distinguished during the digital assessment of land cover around the town of Graaff-Reinet.

Sampling unit	Colour	Vegetation type/Land cover	Soil colour (Munsell)	Cover Class
1	light grey	succulent dwarf shrubland	7.5YR4/4	8
2	grey	dwarf shrubland	7.5YR5/6	9
3	light red and blue	mesic grassland and thicket	n/a	6
4	light red	mesic deciduous thicket	n/a	6
5	white	degraded dwarf shrubland	5YR5/5	6
6	dark blue	shallow water and mud	n/a	n/a
7	light red	shrubland	10YR3/2	1
8	dark red	succulent thicket	10YR5/4	13
9	pink and blue	urban	n/a	n/a
10	clear	succulent dwarf shrubland	7.5YR5/4	8
11	clear brown	open succulent thicket	10YR5/4	13
12	light brown	shrubland	10YR3/2	1

n/a = not available

positional and monitoring information.

The flora of the region is primarily the product of interactions between the steep environmental gradients (Palmer 1988a), palaeoclimatic history (Cowling 1986; Palmer 1988b), recent anthropogenic influence (Acocks 1975) and species responses. These interactions can best be embodied in a community-unit approach to the description of the flora. The Sneeuberg range, which traverses 3224 Graaff-Reinet from north west to south east, divides the arid, alkaline environment of the Camdebo from the wetter, leached conditions of the mountains and high lying plateaux. The cover classes (CC) correlate broadly with one of four phytochoria (Table 3) and the description which follows is based primarily upon the vegetation/landscape units which have been identified using a combination of proxy Landsat data, phytosociological survey and iterative mapping. The cover classes represent broad vegetation categories, developed to provide a rapid assessment of the extent of regional vegetation.

A thirteen class classification system (Table 3)(Appendix Map 2) is presented to describe the vegetation of each of the LSU's on 3224 Graaff-Reinet. Twenty spectral response classes were recognized on the first approximation and seven of these were consolidated with other cover classes. I have retained the original cover class numbers as this ensures repeatable comparison of categories in the field. These will be consolidated in subsequent publications. I do not adhere strictly to the syntaxonomic classification for the study area (Palmer 1988a) as the syntaxa of Werger (1980), Van der Walt (1980) and Acocks (1975) are all taken into consideration. Sub-divisions of CC1, CC8, CC9 and CC13, recognized on the basis of their floristic composition, are not mapped.

Table 3. Major categories recognized in mapping the vegetation of the Camdebo and Sneeuberg regions. (See also Appendix Maps 2)

Cover Class	Vegetation category	Class	Biogeographic affinity
2	Grassy Dwarf Shrubland on footslopes	Karoo Dwarf Shrublands	Karoo-Namib Region
3	Grassy Dwarf Shrubland on dolerite plateaux		
4	Degraded Dwarf Shrublands		
8	Succulent Dwarf Shrublands		
9	Dwarf Shrublands		
6	Riparian Thicket	Riparian Thicket	
13	Succulent Thicket	Sub-tropical Transitional Thicket	Tongaland-Pondoland Regional Mosaic
15	Noorsveld		
1	Montane Grasslands with shrubs and dwarf shrubs	Shrublands	
14	Thorny Shrubland on rocky slopes		Sudano Zambezian region
18	Grassy Open Shrubland		
19	Lowland Grasslands	Grasslands	
19	Dohne Sourveld	Afro-montane Grassland	Afro-montane region
20	Forest	Afro-montane Forest	
20	Scrub Forest		

THE VEGETATION CATEGORIES

I. THE VEGETATION OF THE GREAT ESCARPMENT

(Cover Class 1)

A. Montane Grassland with shrubs and dwarf shrubs

The dolerite intrusion through the sedimentary mudstone and sandstone beds of the Beaufort Group created the Great Escarpment. A distinguishing feature of CC1 is the high altitude and rugged topography, with large dolerite rocks. The vegetation associated with this geology has been termed "Karroid *Merxmuellera* Mountain Veld" (Acocks 1975).

The vegetation of the cover class ranges from a *Themeda triandra/Heteropogon contortus*-dominated Grassland community to a *Euryops oligoglossus*-dominated Shrubland or *Euclea undulata/Rhus erosa* Woody Shrubland. Kloofs are often well wooded with *Olea europaea*-dominated communities. These wooded kloofs reflect as bright green vegetation on the satellite image. Species in the kloofs include *Rhus undulata* and *Rhamnus prinoides*. Dwarf shrubs dominate the mountain slopes in the western and central parts of the largest unit (LSU 323) with shrubs on the highlands in the east, the latter being synonymous with the False Karroid Broken Veld (Acocks 1975).

Synonymy: Karroid *Merxmuellera* Mountain Veld (Acocks 1975); **Rhoetalia ciliata-erosae** (Werger 1978, 1980)

1. Open Shrubland on rocky slopes and ridges

This vegetation occurs on the rocky slopes between 1 100-1 400 m. Typical examples at the Valley of Desolation (LSU 309) are associated with dolerite boulders together with small quantities of lidianite and sandstone. The soils are a shallow Mispah/rock complex with quantities of organic material in the O-horizon, contributing to the high moisture, conductivity and mineral levels (particularly Mg and Ca). These well-drained soils has a moderately alkaline pH (7.1 - 7.8).

Quadrats vary from steeply sloping (1 in 3) convex slopes to flat, plateaux of gentle slope and neutral aspect, and experience high precipitation (±500 mm per annum), in the form of rain, fog and snow.

2. Fire Climax Grasslands

The effect of different management treatments on the vegetation of CC1 (LSU 261) is clearly noticeable at the boundary between the farms Katbosch (3224AA) and Kleinfontein (3224AA) in the Koueveldberge. Quadrats on the farm Katbosch are dominated by *Merxmuellera disticha* whereas on Kleinfontein the adjacent camp contain a *Themeda triandra/Merxmuellera disticha* Grassland. This change in dominance can probably best be accounted for by different management strategies, most likely the application of fire. Other species in the Kleinfontein camp include *Digitaria eriantha, Salvia repens, Protasparagus* spp., *Eragrostis chloromelas, Lycium schizocalyx, Cymbopogon plurinodis, Tragus* spp., *Aloe broomii* and *Rhus erosa. Themeda triandra* canopy cover is ± 60% and total canopy cover ± 90%.

3. Montane Shrubland

On slopes with shale and sandstone parent material, Shrubland predominates. Selective grazing may have accelerated transformation to Dwarf Shrubland, but this is not tested. Area selection is apparent around artificial water points and gates in large camps. Single species herds of domestic grazers are present in almost all situations. This would lend some credence to the hypothesis that the grazing behaviour of domestic ungulates results in a change in the relative abundance of grass or dwarf shrubs (Acocks 1979, McCabe 1987). The drier, warmer, north-facing slopes of "Kleinfontein" are covered with Grassland, whereas the cooler south-east-facing slopes of Essex (LSU 261) contain a Montane Shrubland dominated by *Euryops oligoglossus*.

4. Karroid Shrubland of steep slope with shallow soils.

Very steep convex slopes (30 - 45°) are generally sparsely vegetated, for example Drie Koppen (LSU 323), on the Karoo Nature Reserve. These slopes exhibited erosion patterns and the associated arid-tolerant vegetation. It is certainly justified to recognize these as distinct communities of CC 1.

5. Woody Shrubland

On the southern slopes of the Coetzeesberg (LSU 454), Landsat detected CC13. During ground referencing it was found to be a woody form of CC 1. South of the farm Poplar Grove, the dominant species are *Olea europaea, Rhus undulata* and *A. karroo*. This feature is probably continuous along the southern aspect of the range. There are very few succulents, except for *Aloe broomii*, and the extremely rocky terrain is otherwise vegetated with dwarf shrubs and grass, with *Heteropogon contortus* present in some well-protected situations.

6. Moist sour Grassland

Another variation in CC1 is the high altitude Grassland dominated by *Merxmuellera disticha*. Details of well-preserved examples are given from the LSU 382 (relevé 278) at base of Mount

Marlow.

7. Wetlands

Small, but relatively common wetlands (Gabriel & Talbot 1984), occur throughout the LSU's classified into this category. The wetlands are either permanently or seasonally flooded, and support a flora characteristic of saturated soils. Species include *Scirpus* spp., *Osteospermum* sp., *Lasiospermum bipinnatum*, *Cynodon* sp., *Pentzia globosa*, *Berkheya* sp., *Kyllinga* sp., *Senecio* sp., *Eragrostis* sp., *Walafrida* sp. and *Atriplex semibaccata*.

8. Grassy Shrubland

The Grassy Shrubland is structurally distinguishable from the Karroid Shrubland. The distinction may be a consequence of intensive grazing by domestic ungulates, since soil and ancillary data recorded on the field data sheets suggest that the environmental conditions are comparable. Along a distance gradient from an artificial water point, Karroid Shrubland occur nearer to the water point, whereas Grassy Shrubland occur further away at points less accessible to domestic stock (Palmer 1986). Tentative evidence comes from the floristic condition of two adjacent camps on the farms St. Olives and Louws Kraal. The grazing system being practiced on St. Olives (McCabe 1987) favours the development of a grassy condition, whereas the "selective grazing" practiced on the adjacent property results in a dwarf shrub-dominated Karroid Open Shrubland. This evidence suggests that vegetation transformation in the Open Shrubland may account for the two variations.

The species between the clumps in the Grassy Shrubland include *Eragrostis chloromelas, E. curvula, E. obtusa, Enneapogon scoparius, Themeda triandra, Heteropogon contortus, Cymbopogon plurinodis, Digitaria eriantha, Melica racemosa, Ehrharta calycina, Eustachys mutica* and *Cynodon incompletus*. Grassiness varied from 20 to 75% of canopy cover, and rockiness varied from 20 - 80% of basal cover.

The soil analysis at these sites revealed very high Ca (240ppm) and conductivity (360 uMoh) levels. The soil pH varied from 7.1 in the clumps to 7.8 in the Grassland. Higher Mg levels (80-100 ppm) occur. The soils are a humic Mispah/rock complex, with the dolerite boulders contributing the highest proportion of cover, and possibly influence on soil chemistry.

On the farm Houtconstant, partly in the Camdebo basin, LSU 261 was initially classified as CC6. On visiting the unit, it was found to consists of vegetation akin to that on the hills above the Valley of Desolation and at Waainek on the Karoo Nature Reserve. This is the woody range of CC1, with shrubs in clumps, interspersed with grasses (*Themeda, Eragrostis chloromelas*). Associated woody shrubs include *Osyris lanceolata, Rhus undulata, Rhamnus prinoides* and *Diospyros austro-africana*. The community occurs on the cool southern slopes and on the farm St. Olives.

II. THE VEGETATION OF THE FOOTSLOPES OF THE CAMDEBO (Cover Class 2)

A. Grassy Dwarf Shrubland on foot-slopes

This vegetation category occurs on the "apron" (Roux *et al.* 1981) or footslope (Gabriel & Talbot 1984). It is strongly associated with this topographical unit and is dispersed throughout the region, but has a small total area. It does not extend further up slopes or on the pediments, and is associated with a Mispah/rock complex which occurs at the interface between steep slope and pediment.

The soils are shallow (20cm - 30cm), with the mixing of dolerite rocks of the Stormberg system and the basic sandstones of the Karoo supergroup, resulting in a light brown (5YR 4/3) stoney loam. Organic content in the top soil (where this is still intact) is moderate to low, and pedestal formation is a common phenomenon in this cover class. Canopy cover varies from 50-65% with rockiness (large boulders with a diameter of 0,25-0,5m) accounting for between 5-16% cover. These relatively high canopy cover values are attributable to perennial woody dwarf to medium shrubs. The terrain is gently sloping (1-2%) and the vegetation is an Open, Medium to Dwarf Shrubland. Medium shrubs which may account for up to 30% of canopy cover and are never taller than 1,0 m, while dwarf-shrubs account for 20-30% of canopy cover and are less than 0,3 m high.

The differential species in this cover class are *Rhigozum obovatum, Senecio longiflorus, S. acutifolius, Haworthia viscosa, Sarcocaulon camdeboense* and *Pachypodium succulentum*. The clumps of vegetation also contain species such as *Senecio radicans, Polygala hottentotta, Crassula muscosa, C. tetragona,* and *Sutera* spp. Between the clumps, annual grasses (*Aristida* spp., *Eragrostis* spp.) grow, together with species such as *Aptosimum procumbens, Galenia sarcophylla* and *Blepharis villosa*.

Stem and leaf succulence is a feature of this cover class. Species of the genera *Mesembryanthemum, Crassula* and *Euphorbia* occur, dominated by *Euphorbia mauritanica*. Rare leaf succulents include *Trichodiadema bulbosum* and *Psilocaulon articulatum*. Geophytes are present, particularly *Pachypodium succulentum* and *Lachenalia bowkeri*, both regional endemics.

The limited extent of this cover class throughout 3224 Graaff-Reinet suggest that is important to make an effort to conserve more examples as only an extremely limited example is conserved on the Karoo Nature Reserve.

III. THE VEGETATION OF THE DOLERITE PLATEAUX
(Cover Class 3)

A. Grassy Dwarf Shrubland on dolerite plateaux.

A feature of the geological ontogeny of the Camdebo is the presence of dolerite sills which encircle the plain, and dykes which traverse it. One of the physiographic effects of the sills in this cover class is that a raised platform can form and the parent material from which the soil develops is only of dolerite origin. The presence of the $CaCO_3$ hardpan was confirmed. Van Riet & Minnaar (1977) describe this situation as a Mispah/Nyoka association, being classified as a Swartland form. Saprolite is below the pedocutanic B-horizon in all cases. The presence of a calcareous layer in the B-horizon, and the predominantly non-red colour justifies the classification of MacVicar *et al.* (1977). This phenomenon is obvious on the farm Brooklyn (LSU 274).

Grass species include *Aristida diffusa, A. congesta and Eragrostis bergiana* and *E. lehmanniana*. The ubiquitous dwarf shrubs such as *Pentzia incana* and *Barleria irritans* account for ±20% of canopy cover, whereas grass cover in the extremely dry situation at the time of data collection was ±15%. A differential species is *Gnidia polycephala*. This cover class is readily detectable using the imagery.

IV. THE VEGETATION OF THE BOTTOMLANDS
(Cover Class 4)

A. Degraded Dwarf Shrubland

Classification of the imagery revealed a set of land parcels with light colours on the false colour composite. Initially termed "eroded areas", these parcels were further investigated during the reconnaissance, and defined more clearly. LSU's with low total canopy cover (<20%) are in this class, dropping to below 5%. It is this factor, together with the uniform soil colour, which detracts from the value of detecting this cover class using Landsat MSS data.

Vegetation maps based on Landsat data become unreliable when the vegetation density is less than 20% (McCoy & Witt, 1978; McCoy, 1981). Spectral reflectance under low canopy cover

Figure 1. Degraded Dwarf Shrublands of the bottomlands of the farm Paardekraal (31°53'S, 25°42'E).

values is largely influenced by rock-soil background effects because light colour soils produced a higher Landsat digital count in MSS bands 4, 5 and 6, than the corresponding bands in darker soils (Ezra *et al.* 1984). A comparison between the values obtained in the study by Ezra *et al.* (1984) on bare soil of various colours and on light soils (Palmer 1988c), indicates that the rock-soil background is the predominant influence in bands 4,5 and 6.

The ubiquitous *Acacia karroo* and a dwarf shrub community dominated by *Pentzia incana, Chrysocoma ciliata* or *Eriocephalus ericoides* are reliable features of this cover class, together with common grasses (*Aristida* spp., *Eragrostis* spp.) and dwarf shrubs (*Blepharis* sp., *Lycium schizolcalyx*). The cover class occurs reliably on Quaternary alluvium overlying sandstone. These alluvia are fine-grained duplex soils which are extremely susceptible to erosion. The soils are usually deep (up to 13m) and structureless, being classified by Van Riet & Minnaar (1977) as a Dundee-Limpopo association, with an orthic A-horizon overlying a stratified alluvium. Calcium carbonate is sometimes present as inclusions, but these do not appear to contribute significantly to soil chemistry. The soils exhibited rapid infiltration rates where the A-horizon had not been eroded away.

Numerous alien species are regularly found within this cover class. These include *Tribulus terrestris, Atriplex lindleyi (=Blackiella inflata), Emex australis* and *Boerhavia cardobensis*. In some localities the surface has been disturbed by ploughing (in an attempt to effect re-vegetation), or by planting aliens such as *Agave americana* and *Atriplex nummilaria*. Patchiness may be attributable to the presence of small mammals which modify the habitat. Whistling rats (*Parotomys* spp.), ground squirrels (*Xerus inaurus*) and suricates (*Suricata suricata*) occur, and are capable of transforming the landscape by creating patchy mounds or "heuweltjies".

Sampson (1986) suggests that areas of rill and gully erosion in the upper reaches of the Seekoei river valley (151 km north west of the Camdebo) may have been initiated by XhoiSan (Bushman). Some of the LSU's allocated to this cover class may represent examples of this type of historical human activity. No stone artifacts were found in any significant densities during this study. Another suggestion is that this cover class is a product of selective utilization by domestic livestock in recent historical time.

Synonymy: Pentzio-Chrysocomion (Werger 1980).

V. THE VEGETATION OF THE RIVER BANKS AND STREAMS

(Cover Class 6)

A. Riparian thicket

The vegetation associated with water courses throughout the Camdebo is readily detected, mainly to the high shrub density and the pattern and association of these features. Two major rivers (Sundays and Great Fish) flow through the study area and the vegetation associated with the banks of these rivers, and their tributaries, produce high reflectance values in Band 7. Much of this cover class has been cleared along the main courses of the Great Fish and the Sundays rivers for cultivated lands. This cover class has not been included on the accompanying map.

The vegetation consists of trees and shrubs of the genera, *Acacia, Rhus, Celtis, Lycium, Maytenus, Diospyros*, and *Olea*. The trees may be up to 10m high, with well developed trunks which have persisted through centuries of flooding. The understorey consists of dwarf shrubs, herbs and grasses. Genera include *Gazania, Lycium, Cynodon, Melianthus* and *Salvia*.

Synonymy: Riparian Thicket (Werger 1980).

VI. THE VEGETATION OF THE PEDIMENTS

A. SUCCULENT DWARF SHRUBLAND

(Cover Class 8)

Eberlanzia spinosa-Rosenia humulis **Succulent Dwarf Shrubland of the Camdebo**

An outstanding features of the Camdebo is the extent of the Succulent Dwarf Shrublands, which occur in small patches throughout the pediments, occasionally becoming dominant. Succulent dwarf shrubs are leaf succulents which seldom exceed 0,3 m.

Marloth (1908) recognized the importance of the succulent component in characterizing the karoo flora. He divided the succulents into leaf succulents *(Mesembryanthemum, Augea, Anacampseros, Crassula, and Aloe)* and stem succulents (*Cotyledon, Euphorbia, Stapelia* and Composites)(Table 4). Succulent dwarf shrubs are much branched and single-stemmed, with short (< 2cm) cylindrical succulent leaves. Stem spinescence may be present. The species are all winter flowering, reaching flowering peaks from August to September (Palmer 1981). Many of these species are reported to display the CAM (Crasslucean acid metabolism) photosynthetic pathway. I encountered succulent communities with various proportions of these structural groups throughout the Camdebo. In nearly all cases they are accompanied by dwarf shrubs, grasses, geophytes and annuals.

The Succulent Dwarf Shrubland is restricted to sites where leaf and stem succulents of less than 0,5m high accounted for between 4 and 13 % of canopy cover. The number of species of dwarf succulents ranged from 3 to 9. Common constituents are members of the family Mesembryanthemaceae, namely *Eberlanzia spinosa*, *Psilocaulon absimile*, *Mestoklema tuberosum*, *Drosanthemum* sp., *Delosperma* sp., *Trichodiadema bulbosum*, *Galenia sarcophylla* and *Ruschia unidens*. The genus *Crassula* is almost absent from Succulent Dwarf Shrubland. This is a dominant family in the region, accounting for some 5% of the total number of species on the Karoo Nature Reserve (Palmer 1988d). Aloes are also comparatively rare in this cover class while the stem succulent *Euphorbia* spp. are more common. *E. mauritanica* and *E. ferox* are present, as well as numerous geophytes, including *Ledebouria floribunda*, *Lachenalia* spp., *Albuca altissima*, *A. trichophylla*, *Sarcocaulon camdeboense* and *Gasteria spp.* Other genera which display leaf succulence in this cover class include *Anacampseros telephiastrum*, *Senecio radicans*, *S. acutifolius* and *Salsola aphylla*.

Synonymy: *sensu lato* False Central Lower Karoo (Acocks 1975).

1. *Eberlanzia spinosa* - *Eriocephalus ericoides* **variation**

The category is characterized by the spiny aizoaceous succulent *Eberlanzia spinosa* and the spiny dwarf shrub *Eriocephalus spinescens*. Associated differential genera include *Aptosimum*, *Salsola* and *Hermannia*. In accordance with Werger (1980), Succulent Dwarf Shrublands are on slightly acid to neutral soils with depths varying from 0,3 to 1,0 m. A relatively high silt fraction is a feature of these soils (Palmer 1988c).

Succulent dwarf shrubs account for 30-40 % of canopy cover, with annual grasses, dwarf shrubs and geophytes make up the remainder in that order. The shallow (12cm), weakly structured, brown to yellow duplex soils are derived from pedisediments. *Pachypodium succulentum* and the endemic *Sarcocaulon camdeboense* are present.

Synonymy: *sensu stricto* Eriocepalo-Eberlanzietum (Werger 1980)

2. *Mestoklema tuberosum* **variation**

This variation is dominated by non-spiny leaf succulents, and uncommon. Cover-abundance values for *Pentzia incana* are high, and many spineless, leaf succulents occur. The most frequently occurring taxa are *Mestoklema tuberosum*, *M. illepidum*, *Delosperma* spp., *Trichodiadema bulbosum*, *Drosanthemum* spp. and *Lycium schizocalyx*. Geophytes, including species of the genera *Albuca*, *Bulbine* and *Haemanthus* are well represented but, Crassulaceae are absent.

3. ***Rhigozum obovatum*** **transitional variation**

On the south western section of the Camdebo plain, as well as on the Karoo Nature Reserve, Succulent Dwarf Shrubland is found to contain *Rhigozum obovatum*. The variation is associated with two features: sites where large dolerite boulders have rolled down a slope, and scattered and broken down on the gently sloping terrain; and sites on the pediments where a rock outcrop (usually of extremely resistant sandstone) is present. *R. obovatum* is stunted, seldom exceeding 1,0m in height. This is probably a transitional community, with species common to both the Succulent Thicket and the Succulent Dwarf Shrubland present.

4. ***Psilocaulon articulatum - Salsola aphylla*** **variation**

This variation of the Succulent Dwarf Shrubland is restricted to patches of increased salinization. Roux and Opperman (1986) report that salinization has increased in low lying, badly drained areas. The succulent genera *Drosanthemum, Mestoklema, Trichodiadema* and *Malephora* are also represented. The differential species are *Psilocaulon absimile, P. articulatum* and *Salsola aphylla*. Contrary to Roux & Opperman (1986), I suggest that this is not a response to recent salinization as there are many, established examples throughout the Camdebo adjacent to "healthy" Dwarf Shrubland is intact.

Alien plant species include *Salsola kali, Geigeria filifolia, Atriplex nummilaria* and *A. lindleyi*. These are halophytic aliens, introduced specifically to utilize areas of excessive salinization. Geophytes include species of the genera *Lachenalia, Albuca, Ledebouria* and *Gasteria*. This cover class extends from Rietfontein-vlakte north-west of Cradock, across the Camdebo plains, to east of Aberdeen.

These communities are significant in the agricultural activities of the region, on account of their winter growing and flowering habit. Although the predominantly grazing behaviour of the domestic herbivores has been well demonstrated (Botha *et al.* 1983), there is evidence to suggest that goats and wild ungulates (Brink, pers. comm.) use this community in the winter when the forage value of the other dominant species is low. It is essential to recognize these communities as an integral part of the karoo ecosystem, and to manage, monitor and conserve them effectively. Further conservation of these pediment communities is an urgent priority.

B. THE DWARF SHRUBLANDS

(Cover Class 9).

Acocks (1975) suggests that the False Upper Karoo contains the "most spectacular of all changes in the vegetation of South Africa", and that this is largely due to the aridification of the area, and the subsequent invasion of Grassland by dwarf shrubs of the semi-arid regions. Colonization of areas with reduced vegetative cover by suites of species including *Pentzia incana, P. globosa, Chrysocoma ciliata, Rosenia humulis, Eriocephalus ericoides* and species of the genus *Pteronia* is the suggested mechanism of invasion. Although the Camdebo contains no False Upper Karoo (VT 36) it does contain False Central Lower Karoo (VT 38) which Acocks (1975) neglects to describe in any detail. I assumed that Acocks suggests that the same process of "invasion" is occurring in this area, as he uses the term "False" to describe it.

The Dwarf Shrubland is generally dominated by *Pentzia incana*, a ubiquitous species associated with alkaline soils throughout the Camdebo. It has been necessary to distinguish the components of the Dwarf Shrubland on the presence of other species, and the absence of certain distinctive structural groups (Table 4). The presence of succulence has been adequately dealt with in the CC8. The next group is characterized by a high proportion of annual and weakly perennial grasses and is associated with the alluvial soils of the pediments.

1. The Grassy Dwarf Shrubland (Figure 2).

The composition of the Grassy Dwarf Shrubland differs from the Succulent Dwarf Shrubland in having higher cover-abundance values for grasses. The increased grassiness encourages the summer production of livestock. Prominent grass genera include *Eragrostis, Aristida, Tragus* and *Cynodon*. In the grassiest condition on the eastern extreme of the gradient, these genera are replaced by *Enneapogon, Fingerhuthia* and *Sporobolus*.

A feature in the soil profile of the Grassy Dwarf Shrubland is a $CaC0_3$ hardpan located at approximately 30cm depth. Soil texture is a sandy loam (Palmer 1988) and the colour a yellow brown (10YR 5/4). There is not a well-defined relationship between A-horizon texture (Sa, Si,Cl) and structure (Palmer 1988c).

No single geological formation contributes substantially to the soils of the Dwarf Shrublands, with much of the material derived from mudstones, dolerites and sandstones and termed alluvium. This is distinct from the deep Quaternary alluvium in the Vlekpoort River, and is shallower (seldom more than 30 cm), often with oxidized dolerite inclusions which formed cutans within the profile. Where tested, soils have high infiltration rates. A simple field test

Figure 2. Grassy Dwarf Shrublands.

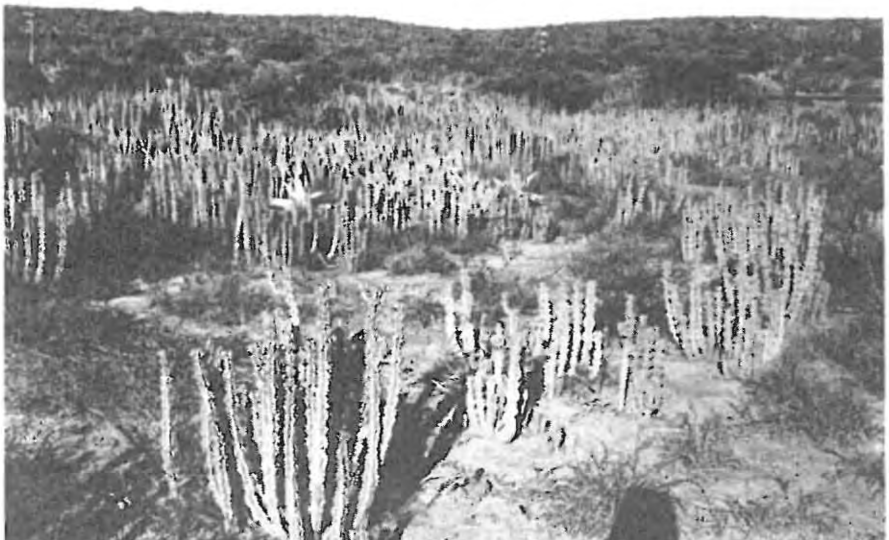

Figure 3. Noorsveld near Jansenville. Species include Euphorbia coerulescens, Portulacaria afra and Pentzia incana.

Table 4. The growth form characteristics of major plant groups in and adjacent to the Nama-Karoo biome

Growth form		Representative genera in the study area
Annual dicot		Tetragonia, Mesembryanthemum, Hypertelis
Geophyte		*Boophane, Ornithogalum*
Annual grass		*Aristida, Eragrostis*
Perennial grass	C3	*Merxmuellera*
	C4	*Panicum, Heteropogon, Themeda, Digitaria*
Sedge		Mariscus, Cyperus, Kyllinga
Dwarfshrub	- deciduous	*Indigofera, Lightfootia*
	- evergreen	*Pentzia, Chrysocoma, Pteronia*
Succulent	- leaf	*Eberlanzia, Portulacaria, Mestoklema*
	- stem	*Euphorbia*
Lichens/mosses		*Usnea*
Lianas		*Rhoicissus, Sarcostemma*
Shrubs	- deciduous	*Acacia, Rhus, Schotia, Grewia, Rhigozum*
	- evergreen	*Pappea, Maytenus, Boscia*

shows that water would percolate through the soil at a rate of ±20 ml/min, compared with the slower infiltration rate of ±4ml/min. in the Succulent Dwarf Shrubland.

Canopy cover varies from ±35% in heavily utilized areas to ±60% in well preserved examples. These relatively high values may account for the spectral homogeneity of LSU's using the manual interpretation technique. The mean canopy cover is ±50% (n=11), whereas in the Succulent Dwarf Shrubland mean canopy cover was ±41% (n= 35).

The *Eragrostis lehmanniana - Pentzia incana* is the dominant association. Accompanying grass species include *Aristida congesta, A. diffusa, Eragrostis curvula, E. obtusa, E. chloromelas, E. bicolor, E. bergiana, Enneapogon scoparius, Digitaria eriantha, Sporobolus fimbriatus, S. ludwigii, Cynodon incompletus, Tragus koeleroides, T. racemosus* and rarely *Merxmuellera disticha* and *Melica racemosa*.

2. Dwarf Shrubland *typicum*

Pentzia incana dominates those quadrats with the highest pH levels (7.5 - 8.0). There are few grasses and succulents, with dwarf shrubs contributing most to canopy cover.

i. ***Pentzia incana-Eriocephalus ericoides*** **variation**

The dwarf shrubs *Pentzia incana, Eriocephalus ericoides, Chrysocoma ciliata, Walafrida geniculata* and *Felicia filifolia* are dominant. Grasses include *Eragrostis obtusa, E. lehmanniana, E. chloromelas, Aristida diffusa* and *A. congesta*.

The canopy cover of the quadrats is relatively high (±48%; n = 8), with the dwarf shrubs accounting for 35-80% of this cover. Soils have a high clay content (±18%). Mudstone contributes to the high incidence of clay, and the soils are alluvial, of mixed origin, with oxidizing mudstone, sandstone and dolerite in the A-horizon. Changing proportions of parent material affects the soil pH and this is one of the features which made classification of the pediment soils most difficult. Accompanying species include *Lightfootia albens, Lycium schizocalyx, Protasparagus acocksii, P. suaveolens, Thesium hystrix* and *Aptosimum procumbens*.

ii. ***Pteronia glauca - Pentzia incana*** **variation**

Pteronia glauca differentiates these Dwarf Shrublands. The quadrats are located on a sandy loam overlying sandstone saprolite. Soils are the Swartland form, Nyoka series (Mac Vicar *et al.* 1977), with $CaCO_3$ in the profile. Canopy cover is low (±28%; n = 3). Soil colour differences account for the recognition of these as different LSU's, with colour ranging from 7.5 YR 4/4 to

10 YR 4/3, being lighter than in other LSUs of CC9.

VI. VEGETATION OF THE CONCAVE SLOPES OF THE GREAT ESCARPMENT (Cover Class 13)

A. Thicket

Cowling (1984) suggests the term Sub-tropical Transitional Thicket to describe the closed, large-leaved shrublands which extend from the Tugela river to the Western Cape. Physiognomically similar communities occur in the study area. Acocks (1975) describes the Succulent Thicket of the study area as Succulent Mountain Scrub (VT 25), and the woody examples as False Karroid Broken Veld (VT 37).

Manual or digital interpretation of the Landsat imagery does not distinguish the variations of CC13 (Palmer 1988e). Tonal differences were used to distinguish between the cover classes containing woody and succulent shrubs, and forest. The distinction between the Succulent, Non-succulent and Riparian Thicket was based on pattern and association. A significant interpretation error occurred in the Shrubland on the Coetzeesberge, which was initially classified as Succulent Thicket.

1. Succulent Thicket

Soils are less alkaline than those of the Dwarf Shrublands, with lower K and Na levels. The associated geology is dolerite boulders overlying sandstone in the west and mudstone in the east. It is difficult to identify a single geological formation contributing to community distribution, but rather a composite of two or more layers of the Karoo Supergroup. Succulent Thicket occurs on concave landforms, with many of the quadrats having a northern or southern aspect. The ground layer between the trees and shrubs is covered by dwarf shrubs of Nama-Karoo affinity. These include *Aizoon rigidum, Galenia sarcophylla, Thesium rigidum* and *Pentzia incana*.

The differential species of the Succulent Thicket are *Portulacaria afra, Grewia robusta, Pappea capensis, Maytenus polyacantha, Euclea undulata, Rhus refracta, Crassula ovata, Rhoicissus tridentata* and *Carissa haematocarpa*. Canopy cover of the vegetation was high (±70%), with shrubs between 1.5 and 2.5m accounting for 30-40% of this cover. The vegetation reflected high digital counts in MSS band 7.

2. Non-succulent Thicket

Portulacaria afra is absent from quadrats in the non-succulent thicket, yet the other species present are associated with it in the Succulent Thicket. The reason for the absence of *P. afra* is suggested as over-utilization by domestic browsers (McCabe pers. comm.).

Surface soils within the clumps are organically rich (±36% carbon), with a neutral pH (7.1). Ca and conductivity levels were the highest recorded in the soil survey (275 ppm and 1137 µm respectively). Sandiness within the clumps were moderately high. Palmer *et al.* (1988) report distinct differences between clump and interclump soils in the Succulent Thicket of the eastern Cape. This trend is further confirmed in this study. Rockiness accounts for 15-40% cover. It is difficult to distinguish this class from CC1 on the basis of tonal differences using the manual interpretation technique. Digital data have not been examined.

Common floristic elements are the perennial woody shrubs and their associated herbs, geophytes and lianas. These woody shrubs include *Rhus undulata* var. *undulata, Grewia occidentalis, G. robusta, Diospyros austro-africanus, D. lycioides, Rhus pentherii, R. erosa, Euclea undulata*. var. *crispa, Dioscorea elephantipes* and *Acacia karroo*. The dwarf shrubs below and between the shrubs include *Pentzia incana, Chrysocoma ciliata, Rhigozum obovatum, Eriocephalus ericoides, Felicia muricata* and *Helichrysum* spp.. Grass species range from annuals such as *Eragrostis obtusa* and *Aristida congesta* to the perennial *Panicum maximum, Heteropogon contortus* and *Digitaria eriantha*. Oxidizing dolerite boulders occur in all the quadrats surveyed, and the soil is a sandy loam of a Mispah-rock complex. The understorey may contain *Sanseveria thyrsiflora, Protasparagus* spp., *Blepharis capensis* and *Senecio* spp.. Leaf succulents such as *Aloe broomii, Crassula rogersii, Ruschia unidens* and *Senecio radicans* are present occasionally in the formation.

VII. THE VEGETATION OF THE ECCA SHALES
(Cover Class 15)

A. Noorsveld

Succulent Thicket in the vicinity of Jansenville (Figure 1) was classified as CC14 following manual interpretation of the false colour imagery. Structurally and floristically this is related to Succulent Thicket, and represents a clear example of the unreliability of Landsat in detecting related vegetation in arid conditions. Quadrats surveyed in the Noorsveld contained many species found in the succulent thicket, including *Portulacaria afra, Rhigozum obovatum, Grewia robusta, Maytenus polyacantha, Euclea undulata, Pappea capensis, Schotia afra and Rhus undulata*. During the ground reference survey, I mapped the extent of this veld type and estimate that the boundaries remain relatively unchanged from those determined by Acocks (1975).

A relationship between the distribution of the Ecca shales (Visser 1984) and the Noorsveld is apparent. *Euphorbia bothae, E. lidenii* and *E. coerulescens* appear to favour the mineralized soils of these mudstones.

Synonymy: *sensu stricto* Noorsveld (Acocks 1975), van der Walt (1968)

VIII. THE VEGETATION OF THE CONVEX SLOPES OF THE SNEEUBERG (Cover Class 14)

A. Thorny Shrubland on rocky slopes

Acocks (1975) regarded this as a product of anthropogenic influence in recent historical time. Van der Walt (1980) views this as Mesic Shrubland. Martin & Noel (1960) regard a similar formation in the Great Fish River valley as a Bushclump Savanna. The latter is more appropriate, as the multi-species clumps are separated by expanses of Grasslands or Dwarf Shrublands. Edwards (1983) suggests the term Open Shrubland to describe a situation in which shrub density is between 1 and 10% of canopy cover. This terminology has been adopted, as it enables one to introduce the use of the prefixes "grassy", "karroid" etc. to the formation. In the use of Edwards (1983) system, it is essential to indicate that percent canopy cover of the 100 m^2 quadrats is not a reflection of per cent canopy cover of the landscape. Clumps were included in the quadrats, and therefore contribute significantly to the floristic classification.

These sites are distinctly different from the Grassy Open Shrubland. The herbaceous layer comprises a mixture of grasses, dwarf shrubs, succulents (Mesembryanthemaceae and Crassulaceae), herbs and geophytes. Conditions appear to be more arid than Open Shrubland. *Pentzia incana* is the most abundant dwarf shrub, with *Enneapogon scoparius* and *Heteropogon contortus* dominating the grassy component.

Examples of this cover class include a wide range of floristic types, but structurally they are related i.e. Grassland or Dwarf Shrubland, with medium density shrubs. The Grass/Dwarf Shrubland may contain a range of structural types from the C4 grasses (*Panicum stapfianum, Setaria sphacellata, Themeda triandra*) to deciduous dwarf shrubs (*Pentzia incana, Chrysocoma ciliata*). This can be further sub-divided on the basis of its floristic composition, as well as the relative proportions or mixes of the various structural classes. Landsat has not enabled clear discrimination within the range of vegetation.

The high canopy cover of *Acacia karroo* probably affects the radiometry of the sites, particularly in Landsat band 7. This cover class has some special significance to vegetation monitoring. In LSU's 400, 401, 405, 407, 409, 415 and 448, which were identified in the south eastern section of Graaff-Reinet 3224, the cover class represents those areas where *Acacia karroo* has started to increase in the Eastern Province Grassland. Acocks (1975) described this as False Thornveld of the Eastern Province (VT 21) and any changes in the extent of these units could be used to describe the pattern of the *A. karroo* behaviour. The increase in woodiness in the eastern section of 3224 Graaff-Reinet is causing concern (Du Toit 1968). Management strategies are available to control this phenomenon (Trollope 1974, Aucamp *et al.* 1983) but there seems to be little enthusiasm for these relatively inexpensive approaches. The use of granular herbicides to control *A. karroo* is becoming more common. Further research on the extent, and expansion, if any, of these LSU's would provide a useful contribution to understanding the dynamics of this species.

A distinctive feature of CC14 in LSU s' 400-409 is the presence of termitaria of the genus Trinervitermes. The presence of this species may be related to the increase in grassiness and the sandier top soil. Vegetation in the road and railway reserves suggest that under judicial management, a *Cymbopogon/Themeda* grassland can develop. The railway reserve in LSU 448 is regularly burnt and fire-adapted grasses are present, and there is a lower incidence of *A. karroo*.

Synonymy: *sensu lato* False Karroid Broken Veld (Acocks 1975); *sensu lato* Mesic Shrubland (Van der Walt 1980)

IX. THE VEGETATION OF THE KATBERG SANDSTONE
(Cover Class 18)

A. Grassy Open Shrubland on sandstone

This is one of the smallest Veld types, measuring some 2250 km^2 (Scheepers 1983) in extent. The visual interpretation of the Landsat imagery detected a distinct unit with very similar boundaries to that mapped by Acocks (1953). During the survey, it was ascertained that much of the vegetation within this unit was in a "healthy" condition, and that Acocks' assumption should not go unchallenged. A relatively high proportion of this veld type is conserved in the Mountain Zebra National Park (MZNP), and the concept "replaced by karoo" should be re-assessed.

Van der Walt (1980) recognized a *Becium burchellianum* community on the plateau on the MZNP, and regards this as a product of localized over-grazing. The floristic information presented by Van der Walt (1980) indicates that quadrats in this community have high cover abundance values for species with the ability to survive in a shallow stoney soil. *B. burchellianum* is a regional endemic, and grows along a north/south gradient between Cradock and Grahamstown (Palmer 1988a). The species appears to be associated with sandstone outcrops which corresponds extremely accurately with the VT 42 and LSU 3224/356.

Differential dwarf shrubs include *Eriocephalus ericoides, Pentzia sphaerocephala, Sutera atropurpurea, Pegolettia retrofracta* and *Becium burchellianum*. The integrity of the association between these species and the LSU is good. Woody shrubs are rare, but include *Rhus erosa* and *R. undulata*. Grasses are abundant, and include *Aristida diffusa, Eragrostis lehmanniana, E. obtusa, Themeda triandra, Heteropogon contortus* and *Tragus koeleroides*.

Synonymy: *sensu stricto* Karroid *Merxmuellera* Mountain Veld replaced by karoo (Acocks 1975).

X. THE VEGETATION OF THE MESIC PEDIMENTS, UPLANDS AND SLOPES (Cover Class 19).

A. Grasslands

Two Grasslands are recognised, Afromontane Grasslands and Lowland Grasslands. The distinction is on the basis of altitude, and the associated effect of low winter temperatures.

Synonymy: Pure Grassveld Types (Acocks 1975)

1. Lowland Grasslands

Situated on the lowland (550-900m) between Bruintjieshoogte and Debe Nek, Acocks' (1975) describes this as the densest grassland in the Republic. Some unique LSU's in the Somerset East area reliably corresponded with the distribution of this grassland, but much of the area has been invaded by *Acacia karroo* and displays a spectral reflectance pattern more akin to Grassy Shrubland.

Soils are low in minerals (Mg, Ca, Na, K and P) with a moderately alkaline pH (6.3) and a relatively high clay fraction (±12%). Above-ground termitaria occur throughout the landscape.

Grass species with high canopy cover values include *Themeda triandra, Eragrostis capensis, Digitaria eriantha, E. chloromelas, E. curvula, E. obtusa, E. plana, Cynodon incompletus, Tragus koeleroides, Cymbopogon plurinodis, Sporobolus fimbriatus, Panicum stapfianum* and *Heteropogon contortus*. Dwarf shrubs found include *Euryops anthemoides, Helichrysum dregeanum, Nenax microphylla, Hermannia althaeoides, Pelargonium abrotanifolium* and *Lycium* *schizocalyx*. These species correspond well with those listed by Acocks (1975) as being diagnostic of the Eastern Province Grassveld.

Synonymy: Eastern Province Grassveld (Acocks 1975)

2. Afromontane Grasslands (Acocks 1975)

Acocks (1975) suggests that the Dohne Sourveld has replaced the forest. Evidence to refute this has been provided by Meadows & Meadows (1988). The floristic description by Acocks (1975) of this formation has not been elaborated upon in this study. The quadrats surveyed confirm his classification, and a second approximation would be more appropriate under the aegis of the Grassland Biome Project. Soil samples from the farm Sterkwater, contained low concentrations of minerals (Mg, Ca, K, Na and P), as well as a low pH (5.4). This suggests leaching of the upper soil and a low nutrient status for these grasslands.

Synonymy: Dohne Sourveld (Acocks 1975)

XI. THE VEGETATION OF THE MESIC SOUTH-FACING SLOPES (Cover Class 20)

A. Forest

A sandstone and shale massif comprises the escarpment and the orographic rainfall which results from this landform accounts for the wetter, cooler conditions which prevail. These conditions are largely responsible for the occurrence of Forest. The Afro-montane element are Forest, Scrub Forest and Montane Grassland.

On the southern slopes of the Bosberg range, a forest with Afromontane affinity occurs. The wettest form occurs along the drainage lines, where *Calodendrum capense, Celtis africana, Rhus baurii* and *Podocarpus falcatus*, are found. The Landsat image detects a much more extensive band of vegetation in this region. Once again it is not possible to distinguish the various structural classes of bright vegetation using the imagery only. The contrast between *P. afra* dominated vegetation and Forest is insufficient to differentiate between the two using standard products. Ground referencing reveals the difference, and it is therefore essential to visit each LSU to describe its status.

Scrub Forest accounts for the remainder of the forest type and is distinguished by the presence of *Ziziphus mucronata, Olea europaea* and *Ptaeroxylon obliquum*. Accompanying species include *Leucosidia sericea, Aloe ferox, Euryops spp., Euclea undulata, Scutia myrtina, Grewia robusta* and

G. occidentalis. Other woody species in the scrub forest are *Rhus macowanii, Acacia karroo, Maytenus heterophylla, Osyris lanceolata, Rhus longispina, Maytenus polyacantha* and *Cussonia paniculata*.

CONCLUSIONS

By interpreting pattern and by association, I have delineated topographically and geologically related polygons. I describe features of the physiography, geology and soils of these polygons which make them unique. The information collected in each of these polygons has enabled me to prepare an *a posteriori* classification of the vegetative cover. This is described as a series of cover classes, each one of which contains many floristic elements. Some of these floristic elements are common to different cover classes and they should therefore not be regarded as unique (e.g. *Pentzia-Eriocephalus* elements are common in CC1, CC4, CC8 and CC9). On examination of the flora, I have not found the technique reliable in detecting the floristically defined plant communities. Manual interpretation (eye-balling) of the Landsat standard products has not proved a reliable method of detecting specific plant communities in the karoo biome (Palmer 1988e) with the exception of the Succulent Thicket/Dwarf Shrubland boundary. This is distinct on both the winter and summer imagery, as is the Forest/Dwarf Shrubland boundary.

Griffiths (1986) reports a lack of success with mapping rangeland vegetation in northern Kenya, stating that the vegetation could not be mapped by visual appraisal of Landsat false colour imagery due to the sparse plant cover and its spectral similarity with bare soil. Saint (pers. comm.) reports a similar experience with Landsat MSS false colour imagery when mapping vegetation in the Ivory Coast. His recommendation is to establish a more precise radiometric model of the phenology of the vegetation using earth-based radiometers. This would enhance the predictive value of Landsat MSS, TM and Spot data for natural vegetation.

Landsat Sampling Unit should be allocated unique reference numbers with Natural Resource Inventory Worksheets being completed for each LSU. This information will be stored in a database, for later analysis in conjunction with earth-based radiometric data.

Numerous un-tested hypotheses on the origins of the regional flora are presented by Acocks (1953,1975,1979), and a new, refreshing look at the flora is required. The environmental gradients (altitude, rainfall, soils) contribute to vegetation heterogeneity. A two-dimensional aridity gradient runs from west to east (with wetter conditions in the east) and from pediment to upland. The latter gradient is exaggerated by a tendency for the pediments to be drier, having soils with high infiltration rates and low organics in the O-horizon. It is the gradient responsible for differentiating between communities within the cover classes recognized.

Mimicking the grazing behaviour of the Cape mountain zebra on the Mountain Zebra National Park and the Karoo Nature Reserve may represent a valuable model for the management of the Dwarf Shrublands. In summer, the zebra spend most time grazing on the high altitude Grasslands and Shrublands, retreating to the pediments during winter. This relieves the Grassy Shrublands of the mountains of grazing pressure and loads the Dwarf Shrublands of the pediments, where protein content of woody shrubs is comparable to, or better than that of dead grass. In contrast, experiments at the Agricultural Research Station at Middelburg revealed that if Montane Grassland is grazed continuously during summer (Aug-Jan), it degenerates to a Dwarf Shrubland. If it is utilized only in winter (Feb-July) it retains its grassy nature. It is possible that excessive utilization by short grass grazers (sheep) on these grasslands during summer, may transform a Grassland to a Dwarf Shrubland. Trollip (pers. comm.) has demonstrated that in the high altitude, high rainfall area on the Compassberg, it is possible to promote the formation of a Grassland using a combination of fire and non-selective grazing.

Experiments on the Dwarf Shrublands of the pediments at Middelburg have not yielded comparable results. It appears that the nature of the Dwarf Shrubland, its geological origin, substrate, aridity (with organics being constantly removed by wind), varying pH and erodability account for much of the variation in its floristic composition and structure. Although it may look uniform to the untrained eye, it displays remarkable structure heterogeneity.

Acocks (1953), De Klerk (1947) and Tidmarsh (1948) have left us with a conceptual legacy of man-induced diversity. Let us escape from the view of seeing the karoo as an advancing desert. The vegetation must be seen as a product of the many variables operating in an environment, and not a consequence of some anthropogenic activity.

ACKNOWLEDGEMENTS

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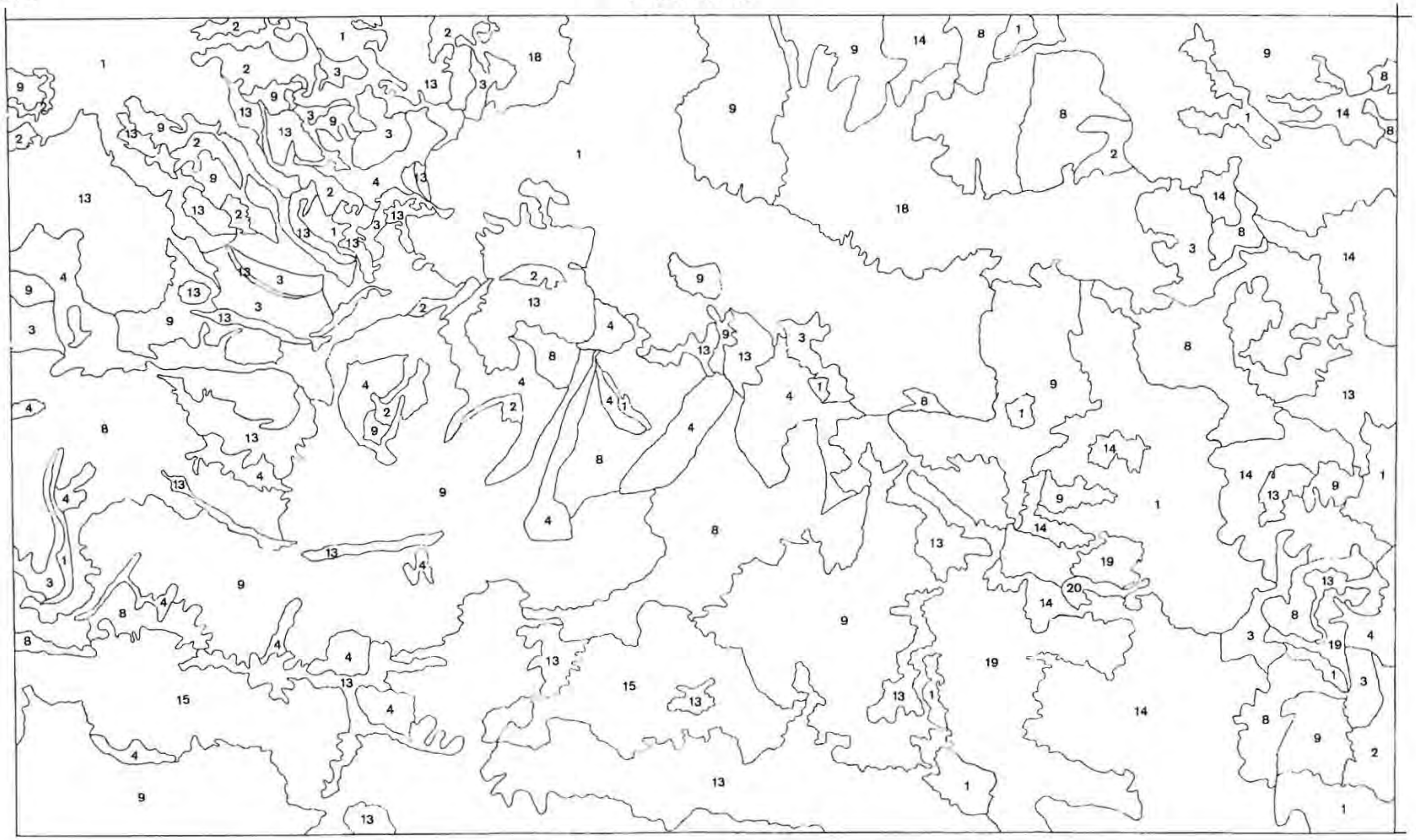
3224 GRAAFF-REINET

VEGETATION



KAROO DWARF SHRUBLANDS

- 8 Succulent Dwarf Shrubland
- 9 Dwarf Shrubland including Grassy Dwarf Shrubland
- 2 Grassy Dwarf Shrubland on foot slopes
- 3 Grassy Dwarf Shrubland on dolerite plateaux
- 4 Degraded Dwarf Shrubland

KAROO SHRUBLANDS

- 1 Montane Grassland with shrubs and dwarf shrubs
- 18 Grassy Open Shrubland on sandstone
- 14 Thorny Shrubland on rocky slopes

SUB-TROPICAL TRANSITIONAL THICKET

- 13 Succulent Thicket
- 15 Noorsveld

GRASSLANDS

- 19 Grassland

AFROMONTANE FOREST

- 20 Undifferentiated Forest

Scale
0 20
km

Landsat MSS imagery was used to determine the boundaries of the various classes, as part of a project undertaken by the Department of Plant Sciences, Rhodes University, the Cape Department of Nature & Environmental Conservation and the Botanical Research Institute, for the National Committee for Remote Sensing (PRD:CSIR).

ECOCLASS: Landscape classification using an expert system

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ABSTRACT

ECOCLASS was developed using augmented PROLOG to aid in the classification of units in a land resource inventory of the semi-arid Karoo region of southern Africa. The units are identified from three-band colour composites of Landsat MSS data, and then each classified with ECOCLASS using data from published inventories of geology, soil, geomorphology, climate and vegetation. The system provides for a four-tier hierarchical classification of the Landsat sampling units. "Domain" is the broad climatic separation of the region; "ecotope" defines the separation of units on the basis of landform and macroclimate; "identified-as" differentiates units on soil chemistry, erosion factors and structural attributes of the vegetation; "community-is" defines the floristic elements which provide the vegetation classification of the unit. ECOCLASS also provides opportunity for developing testable hypotheses that can be incorporated into the classification system after testing.

INTRODUCTION

Responsible natural resource use depends largely on accurate inventories, which implies the creation of a land classification system[1], because an inventory without a classification is an unorganized list. Recent developments in landscape ecology suggest that vegetation mosaic in any landscape is a function of environmental variation and historic disturbance[2] and these relationships between spatial pattern and ecological processes do not occur simultaneously or at the same rate[3]. It has become imperative to consider the predominant landscape, system and community processes in preparing landscape classification systems. This requires that the classification system should be open-ended and flexible, providing the opportunity for incorporating new information at any point.

The development of natural resource classification systems requires a synthesis of the landscape processes and system function. Generally, the specialists in the disciplines associated with each resource have an understanding which supercedes that of specialists from other disciplines. This is particularly pertinent when one encounters the resource classification systems developed by botanists, pedologists, hydrologists, geologists and climatologists in a vast natural region such as the Karoo. It is difficult to find any one individual suitably qualified to undertake synthesis, although ecologists tend to assume this responsibility.

Decision making at any level in this region is dependent on the synthesis of input from this variety of sources. The fragility of the resource as well as the vagaries of climate, make the Karoo a region that should be enjoying research priority. The initiation of the National Grazing Strategy[4] and the Karoo Biome Programme[5] represent steps at establishing research priorities in this region. However, the development of classification systems by a range of specialists, does not provide an integrated picture of the resource. By using a PC-based expert system (APES), it has been possible to initiate the establishment of a classification system for the resource base in the Karoo. This system incorporates information from geology, soils, vegetation and climate.

Lotspeich and Platts[1] have devised a very useful and practical system for land classification. The highest level is that of "domain", and is based on a broad climatic separation of arid and humid regions. For the purposes of this paper the 40 000 km^2 I am dealing with is in the arid to semi-arid Karoo-Namib Domain. The second level of the land classification system[1] is the "province", in which large landforms can be delineated. It is at this juncture that the first level decisions become important in ECOCLASS.

The spectral reflectance data recorded by the Landsat multi-spectral scanner are the products of a multiplicity of resources occurring within the unit. High spectral reflectance values in band 7 of Landsat probably correspond to bright green vegetation; dominance of band 5 depicts geological phenomena; and very low reflectance values, with possible absorbance, are encountered on the deep, alluvial soils of the bottomlands. It is dangerous to develop different classification systems for vegetation, geology or soil using the same Landsat scene processed in the same manner. It is impossible to interpret the spectral reflectance patterns of a classified Landsat scene using the information from only one discipline. ECOCLASS makes use of the classification systems developed by experts in the fields of geomorphology, geology, pedology and vegetation science, to prepare a classification of each Landsat sampling unit.

Expert-system technology has been applied in the development of programs to aid in the identification of biological material[6,7] and ecological decision making[8,9]. These developments have been undertaken by specialists who wish to transfer their judgemental or heuristic knowledge to other users. The developers in these instances have used the Dempster-Schafer theory of evidence[10], or the more familiar Bayesian inference. The former, a generalization of classical probability theory, has been used in preparing a river classification system for river conservation in southern Africa[11]. The latter is more suited to making use of existing knowledge, rather than capture the knowledge which has not yet been synthesized. It also does not cope with uncertainty.

METHODS

Augmented PROLOG for Expert Systems (APES)[12] is a collection of modules written in PROLOG. This language, according to Noble[8], is one of the "real" expert system languages and the modules can be combined in a variety of ways to construct a range of logic programming environments. A major advantage of APES is that once the syntax has been mastered, it is possible to prepare the rule-base using any ASCII editor, and then to load the "program" using the APES "compiler". The internal editor is clumsy and slow, making interaction wasteful. However, viewing it as a compiler is far more efficient.

A prerequisite for using ECOCLASS is the preparation of a map of the relatively homogeneous Landsat Sampling Units (LSU) at a scale of 1:250 000 and the allocation of a unique reference number to each LSU. The first relationship in ECOCLASS defines the "ecotope" or class of land in terms of the macroclimate (including where necessary, aspect), terrain form and soil type[13] for each LSU. ECOCLASS prompts the classifier with a menu of the landform associated with the LSU. The recognized landform classification is according to Scheepers[14] and includes the categories plateau; upper, middle and lower pediment; bottomland; convex and concave slope; and rocky ridge. I have defined nine ecotopes in the Camdebo and Sneeuberg region (Table 1).

Once the conditions fulfilling the "ecotope" classification of the site have been complied with, it is possible to proceed to the next relationship in ECOCLASS, namely "identified-as". This relationship deals with the physiognomic or structural attributes of the vegetation. Questions relate to the geology at the site, the erosion status of the site, the soil pH and structure, as well as basic questions relating to the vegetation structure i.e. the presence of grass, dwarf shrubs, thicket or succulent dwarf shrubs (Table 2).

The structural nomenclature of "identified-as" is derived from numerous authors[15,16,17], with the geological classification system developed by Johnson & Keyser[18].

Following a syntaxonomical treatment of the vegetation[17], two further relationships, namely, "community-is" and "variation-is", were developed. These relationships necessitate a knowledge of the floristics of the region, which is generally only applicable to botanists. The completion of relationships one and two provide a useful resource map of the entire region.

RESULTS

The system was used to classify LSU's during a natural resource inventory of the Camdebo and Sneeuberg region of the karoo biome. Field data sheets had been completed for 149 of the 448 LSU's identified, and these LSU's were classified to the level of "community-is". The remaining LSU's were classified to the level "identified-as", which corresponds to a structural classification system for the vegetation of the study area.

CONCLUSIONS

Developing ECOCLASS has assisted in solving some of the vegetation map preparation problems encountered in the Karoo Region, particularly after the poor results obtained by interpreting Landsat MSS data in relation to vegetation only[19]. In semi-arid areas, where vegetation cover is low, soil background colour masks the effect of vegetation on the spectral reflectance characteristics. ECOCLASS has enabled me to further reduce my ground reference data to predict vegetation from a combination of landform, soil and climatic characteristics. It had assisted in classifying extensive natural areas without the necessity of visiting each and every Landsat Sampling Unit. ECOCLASS aims to provide "deeper

Table 1. Ecotopes of the Camdebo region of the Karoo-Namib domain.

Ecotope	Landform	Climate	Soil	Geology
1	convex slope	warm, wet	rocky Mispah	dolerite sandstone
2	convex slope	warm, wet	stoney Mispah	mudstone sandstone
3	convex slope	warm, dry	stoney Mispah	sandstone
4	concave slope	cool, wet	rocky Mispah	dolerite mudstone
5	pediment	warm, dry	sandy loam	alluvium
6	plateau	cool, wet	rocky Mispah	dolerite sandstone
7	bottomland	warm, dry	structureless alluvium	alluvium
8	footslope	warm, dry	rocky Mispah	dolerite sandstone
9	rocky ridge	warm, dry	rocky Mispah	dolerite

Table 2. Portion of ECOCLASS which provides for the classification of succulent dwarf shrubland in the Camdebo region of the Karoo-Namib domain.

```
((ecotope _LSU warm-wet-slope-with-Mispah-rock-complex)
 (is-landform-at _type _LSU)
 (is-landform-at convex-slope _LSU)
 (is-slope-at steep _LSU)
 (is-aspect-at variable _LSU)
 (is-geology-at dolerite-with-sandstone-and-lidianite _LSU))
((ecotope _LSU warm-wet-slope-with-stoney-Mispah)
 (is-landform-at _type _LSU)
 (is-landform-at convex-slope _LSU)
 (is-slope-at steep _LSU)
 (is-aspect-at variable _LSU)
 (is-geology-at sandstone-mudstone _LSU))
((ecotope _LSU warm-dry-slope-with-stoney-Mispah)
 (is-landform-at _type _LSU)
 (is-landform-at convex-slope _LSU)
 (is-slope-at steep _LSU)
 (is-aspect-at variable _LSU)
 (is-geology-at sandstone _LSU))
((ecotope _LSU cool-wet-slope)
 (is-landform-at _type _LSU)
 (is-landform-at concave-slope)
 (is-slope-at steep _LSU)
 (is-aspect-at north-or-south _LSU)
 (is-geology-at dolerite-and-mudstone _LSU))
((ecotope _LSU dry-pediment-with-shallow-soil)
 (is-landform-at _type _LSU)
 (is-landform-at pediment _LSU)
 (is-slope-at gentle _LSU)
 (is-aspect-at neutral _LSU)
 (is-soil-type-at sandy-alluvium _LSU))
((identified-as _LSU karroid-open-shrubland)
 (ecotope _LSU warm-wet-slope-with-stoney-Mispah)
 (_LSU dwarf-shrubs-at))
((identified-as _LSU grassy-open-shrubland)
 (ecotope _LSU warm-wet-slope-with-Mispah-rock-complex)
 (_LSU much-grass-at))
((identified-as _LSU montane-dwarf-shrubland)
 (ecotope _LSU warm-dry-slope-with-stoney-Mispah)
 (dwarf-shrubs-at many _LSU))
((identified-as _LSU montane-grassland)
 (ecotope _LSU warm-dry-slope-on-stoney-Mispah)
 (grassy-at very _LSU))
((identified-as _LSU degraded-dwarf-shrubland)
 (ecotope _LSU dry-pediment-with-shallow-soil)
 (erosion-at severe _LSU))
((identified-as _LSU grassy-dwarf-shrubland)
 (ecotope _LSU dry-pediment-with-shallow-soil)
 (geology-at sandstone _LSU))
((identified-as _LSU grassy-dwarf-shrubland)
 (ecotope _LSU dry-pediment-with-shallow-soil)
 (soil-pH-at basic _LSU)
```

```
 (has-CaCo3-layer-at-30cm _LSU))
((identified-as _LSU succulent-dwarf-shrubland)
 (ecotope _LSU dry-pediment-with-shallow-soil)
 (soil-pH-at acidic _LSU))
((identified-as _LSU dwarf-shrubland)
 (ecotope _LSU dry-pediment-with-shallow-soil)
 (soil-pH-at basic _LSU)
 (NOT has-CaCo3-layer-at-30cm _LSU))
((community-is _LSU Eberlanzia-Rosenia)
 (identified-as _LSU succulent-dwarf-shrubland)
 (is-species-at _type _LSU)
 (is-species-at Eberlanzia-Rosenia _LSU))
((community-is _LSU Psilocaulon-Salsola)
 (identified-as _LSU succulent-dwarf-shrubland)
 (is-species-at _type _LSU)
 (is-species-at Psilocaulon-Salsola _LSU))
((variation-is _LSU Eriocephalus-inops)
 (community-is _LSU Eberlanzia-Rosenia)
 (species-at _type _LSU)
 (species-at Eriocephalus-sp _LSU))
((variation-is _LSU Mestoklema-typicum)
 (community-is _LSU Eberlanzia-Rosenia)
 (species-at _type _LSU)
 (species-at Mestoklema-sp _LSU))
((variation-is _LSU Rhigozum-obovatum)
 (community-is _LSU Eberlanzia-Rosenia)
 (species-at _type _LSU)
 (species-at Rhigozum-obovatum _LSU))
((variation-is _LSU Eberlanzia-typicum)
 (community-is _LSU Eberlanzia-Rosenia)
 (species-at _type _LSU)
 (species-at Eberlanzia-dominant _LSU))
((dict community-is))
((dict variation-is))
((dict identified-as))
((dict ecotope))
((in-menu is-species-at (_type _LSU) (_type) ((Eberlanzia-Rosenia Psilocaulon-Salsola )
species-present 10 25 2 25)))
((in-menu species-at (_type _LSU) (_type) ((Eriocephalus-sp Mestoklema-sp
Eberlanzia-dominant Rhigozum-obovatum) species-present 10 25 4 25)))
((in-menu is-landform-at (_type _LSU) (_type) ((convex-slope concave-slope pediment
plateau footslope rocky-ridge bottomland) landform 10 25 7 14)))
```

knowledge"[8] to the classifier about some of the processes operating in the system.

The system has had the advantage of stimulating the development of testable hypotheses about vegetation related phenonema in the region. Particular mention should be made of the relationship between the presence of succulent shrubs and dwarf shrubs and soil pH. This hypothesis is currently being tested.

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GENERAL DISCUSSION AND CONCLUSIONS

This study provides further insights into the vegetation of the Camdebo and Sneeuberg regions, with many of the objectives having been achieved. I do not provide detailed discussion in this section, as the abstracts and summaries of the various papers include much of what there is to say. I prefer rather to briefly summarize the findings, to elaborate on the short-comings of the methods used and data collected during the study, and to discuss the direction of future research which could be undertaken in the region.

The vegetation classification provides a framework for the development of testable hypotheses on vegetation/environment interactions. The classification embodies the sub-division of the vegetation of the region into classes on the basis of phytogeographical affinity, into orders based on broad floristic and structural attributes, and into communities based on floristic composition. By using indirect methods, this scheme interprets the influence of some of the broad environmental gradients on the vegetation.

The classification has proved useful in the preparation of a description of the vegetation of a small nature reserve in the study area, giving directions which management should follow in applying treatments to the vegetation. The inadequate conservation of the Succulent Dwarf Shrublands is emphasized. The assessment of the total floristic information shows that the conservation areas are not representative of the regional flora. The study of the plant-soil interaction provides some insight into one of the environmental gradients operating in the system.

The qualitative model of the vegetation history emphasizes the fact that existing environmental considerations are not the only factors that must be taken into account when developing a qualitative ecosystem model. The fact that I use the biome concept in the development of my descriptive model may elicit criticism, but biome boundaries are based on more objective methods than those of the phytochoria.

The quantitative assessment of Landsat MSS data shows that these data must be viewed with caution when preparing regional vegetation maps. The data provide an objective method for selecting sample sites or Landsat Sampling Units. However, when defining vegetation boundaries it is less useful, particularly in sparsely vegetated landscapes where the spectral reflectances are largely influenced by abiotic factors.

The comparison between the *a posteriori* classification and that developed using the methods of the Zürich Montpellier school suggests that the former may be a useful method for determining the extent and distribution of plant communities in extensive, semi-arid regions.

The *a posteriori* method does not stand up to the rigid disciplines of the scientific method and must be viewed within these limitations. ECOCLASS represents an effort to integrate the findings of Parts I and II, and expert systems deserve more attention in the development of qualitative ecosystem models. The development of this model will proceed, with each step being tested before incorporation.

Although indirect gradient analysis continues to provide results which approximate broad environmental gradients, the criticism of the "community unit" and "individualistic" concepts (Shipley & Keddy 1987) emphasizes the danger of over-simplifying ecosystem structure by interpreting gradients using restricted environmental data. A feature of the methodology of the Zürich-Montpellier school is the indirect manner in which environmental data are collected, and the restricted predictive value which interpretation of these data have. The hierarchical vegetation hypothesis presented in this study, having used these methods, suffers from these limitations. Without an effort to test the nature of the environmental factors which determine community distribution, the hypothesis remains untested. In using ordination procedures, specifically Decorana and Twinspan, to develop this vegetation hypothesis, I realized the limitations of these methods. Although I deal with this specifically in the thesis, I wish to emphasize the fact that these procedures were only used to develop an initial classification of the data set. These data were extensively rearranged according to the methods of the Zürich Montpellier school. Decorana and Twinspan should be viewed as tools to assist in the development of hypotheses.

The sample size used in the soil analysis is inadequate for detailed hypothesis testing, although it has provided an adequate testable model for certain components. These include the reliability of the relationship between the Succulent Dwarf Shrubland and soil chemistry, which should be tested using direct methods. The relationship between grassiness and the presence of a shallow limestone layer suggest that rehabilitation of Degraded Dwarf Shrublands to Grassy Dwarf Shrubland will only be possible if certain soil and moisture conditions are qualified.

I support the view that an understanding of community composition should be based on a series of multiple working hypotheses (Shipley & Keddy 1987). By multiple working hypotheses, I understand different research efforts at the level of the landscape, the community and the taxon. Other hypotheses which need further testing include the impact of the various land-use strategies on the vegetation of the region. In the term land-use strategies, I include all the livestock management systems currently being practiced on private land. This programme would be an ambitious one, in which permanent, experimental plots and exclosures are established on a range of land parcels. Preliminary results of an assessment of eight data sets collected on the farm Ordonantie from 1950 to 1988, following Tidmarsh & Havenga (1955), suggest that the livestock management system practiced on that property are not having a detectable impact on vegetation composition. For efficient research of this nature to continue, a classification of land-use practiced in the region is needed as the literature does not elaborate on the differences between the models which land managers apply.

The limitations of Landsat MSS data are not new and merely corroborate those of northern hemisphere researchers. I include this work as it contains valuable spectral reflectance patterns for southern African plant communities. The subjectiveness of the *a posteriori* vegetation classification detracts from its value, but does provide the opportunity for comparison with other subjective mapping exercises undertaken in the study area. These comparisons may assist in assessing the validity of the the suggestions about karoo invasion (Acocks 1975). ECOCLASS has not been adequately tested, but by its very nature it is open-ended, enabling modification or the incorporation of new testable hypotheses.

Quality data on historical land-use was seldom found at sites surveyed in this study, and more elaborate hypothesis testing is necessary if the methods of the Zürich Montpellier school are to be used to develop predictive models. I suggest that a good starting point for testing hypotheses at the community level is to develop a set of effective vegetation monitoring techniques. The efforts of Dyer (1937), Tidmarsh & Havenga (1955), Roux (1963), Vorster (1982) and Mentis (1984) are useful contributions. More clarity on the interpretation of these techniques is required as no statement about change, or lack thereof, can be prepared without the firm basis of a statistically repeatable methodology.

There remains a need for the accumulation of more relevés and the synthesis of total floristic data from other studies in the Karoo, providing an improved description of the plant communities throughout the region. This should continue within the methods and techniques of the Zürich-Montpellier school, which has proved to be an exciting tool for vegetation description. The inventory should proceed with the judicious use of satellite imagery, and other products of remote sensing, to establish regional distribution patterns of the communities. The continued use of satellite imagery for vegetation reconnaissance in this semi-arid region must proceed with caution in line with the finding of this study.

Bearing in mind that many ecosystem processes are operating at a landscape scale, an improved landscape classification system for the entire region is required. The role of sediment transport, by both wind and water, in supplying nutrients to pediments and bottomlands, requires research attention.

Although the assessment of digital data showed that the predictiveness of Landsat MSS data is poor, it has been possible to produce vegetation maps. This has been accomplished by an iterative improvement in the LSU classification procedure using rules of association; information from the Natural Resource Inventory Worksheet; and correlation with published material (Acocks 1975, Van der Walt 1980). Further development of expert system-based classification systems for natural resource classification must proceed.

Manual interpretation of Landsat MSS data does not provide a reliable model for predicting and mapping the plant communities of the Karoo when used in isolation. The MSS data provides the boundaries of sampling units, which may be used as sites for the collection of data for a Natural Resource Inventory. When these LSU's are classified according to the attributes recorded on Natural Resource Inventory Worksheets, a more meaningful use of the products of remote sensing may develop. Future research should be undertaken to:

a) ascertain which attributes of a site show the strongest correlation to changes in spectral reflectance patterns? This has not been undertaken in southern Africa, and could best be achieved using an earth-based radiometer (G. Saint personal communication). It would then be possible to prepare details of the most sensitive attributes to measure at each inventory site. Soil colour, texture and moisture are three major variables which appear to influence spectral reflectance in the semi-arid region of southern Africa.
b) develop a multi-temporal model of the spectral reflectance characteristics of sensitive sites in the semi-arid region. This should be carried out using a radiometer, with the view to providing a baseline for monitoring possible large scale transformations due to anthropogenic influences.

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Appendix Table 1. The differential and companion species of the Grasslands of the Sneeuberg region.

Class	I																	
Order	A						B											
Community	1			2			1											
Relevé number	2	1	2	2	2	2	2	1	1	1	2	2	2	2	2	2	2	2
	7	9	7	7	7	2	4	9	9	2	1	1	3	7	1	2	3	4
	4	4	5	2	3	0	9	1	3	5	8	9	3	8	7	3	4	1
Differential species of community IA1																		
Helichrysum nudifolium		+	r											r				
Oxalis bowiei		r	r															
Indigofera rugosa		+																
Diascia capsularis		r																
Pelargonium abrotanifolium		r																
Protasparagus thunbergii		r																
Cotula sororia		r																
Schismus inermis		r							+									
Senecio pterophorus			+															
Elionurus argenteus			r															
Differential species of community IA2																		
Hyparrhenia hirta					+													
Euryops tenuissimus					+													
Tarconanthus camphoratus					1													
Differential species of community IB1																		
Merxmuellera disticha						1	+	m	+	4	3	b	4	3	3	3	3	b
Tragus koeleroides								a	1		+					r	+	+
Elytropappus rhinocerotis							r	+					+	r		r		
Pentzia globosa							+		r								r	
Nenax microphylla							r		r	r								
Felicia filifolia								m			r	r		+				
Diospyros austro-africana					+			+		1				1				
Rhus erosa					+			+		+	+		+					
Heteropogon contortus								1			+			+				
Aristida diffusa							+	+						1			r	
Cymbopogon plurinodis										r	+		+	+				
Eriocephalus ericoides														a		+		+
Salvia repens															+		r	+
Differential species of communities IA1, IA2 & IB1																		
Themeda triandra	3	1	4	3	m			+	+	r	+		+	+	+			
Eragrostis chloromelas		4	+	3	3	r	m	b	3		r	r		1	m		1	3
Passerina montana		+				+	r		m			+						
Eragrostis curvula	b					r	m									+		+
Tetrachne dregei			+			r	m							+				
Melica decumbens		+				r	r								r			

Companion species																	
Chrysocoma ciliata				+			+	r		r	1		r	r			
Walafrida geniculata					r		+	+			r					+	
Pentzia incana					r									r		+	
Lycium schizocalyx	+				1									r	+		
Digitaria eriantha	3													+			
Setaria sphacelata			r										r				
Rosenia humulis																r	r
Helichrysum dregeanum										r							+
Felicia muricata						+										r	
Euclea crispa							r					+					
Scabiosa columbaria		+						+									
Aristida congesta							r									+	
Indigofera sessilifolia							+			r							
Trichodiadema sp.								+					+	r			
Gazania sp.						+	+										
Aloe broomii											+	r					

240 cont

Infrequent species

Aptosimum procumbens (217,r), Arctotis sulcocarpa (223,r), Argyrolobium collinum (249,r), Asclepias (arp1297) (193,+), Aspalathus sp. (arp1329) (193,+), Asclepias sp. (274,+), Berkheya sp. (278,+), Bromus sp. (194,r), Convolvulus sagittatus (193,+), Cotyledon orbiculata (191,+),Crassula capitella (191,r), Cucurbitaceae (arp1502) (217,r), Cynodon incompletus (234,+), Cynodon dactylon (217,3), Dianthus namaensis (193,r), Diospyros lyciodes (233,+), Diospyros sp. (arp1499) (218,+), Eragrostis bergiana (249,+), Eragrostis lehmanniana (234,+), Euryops anthemoides (241,+), Euryops oligoglossus (219,a), Euryops sp. (arp1322)(193,1), Ehrharta calycina (125,+), Euphorbia mauretanica (223,r), Felicia muricata (234,r), Geigeria filifolia (193,+), Helichnotrichnon sp. (arp1304) (193,r), Hermannia coccocarpa (218,r), Hermannia sp. (arp1561) (241,r), Hermannia sp. (arp1303)(193,r), Helichrysum rosum (191,r),Helichrysum sp. (arp1325) (193,+), Helichrysum sp. (arp1299) (193,+), Helichrysum sp. (194,r), Heliophila sp. (arp1268) (191,r), Hibiscus pusillus (278,+), Homeria pallens (234,r), Hypoxis sp. cf argenta (217,r), Karroochloa purpurea (249,r), Lasiospermum bipinnatum (217,r), Lepidium divaricatum (217,+), Liliaceae (arp1272) (191,r), Lightfootia sp. (arp1327) (193,+), Limeum aethiopicum (249,r), Lotononis sp. (193,r), Maytenus polyacantha (191,r), Malephora sp. (191,+),Melolobium candicans (249,r), Mestoklema tuberosum (125,+),Melolobium microphyllum (217,r), Moquinella rubra (278,r), Myrsine africana (233,r), Osyris lanceolata (233,r), Pelargonium reniforme (191,r),Pelargonium myrrhifolium (191,+),Pelargonium sp.(arp1323) (193,r), Pentzia sp. (arp 1495) (218,1), Phymaspermum sp. (arp1326) (193,r), Polygala leptophylla (249,r), Pterothrix spinescens (249,r), Protasparagus suaveolens (278,+), Protasparagus subulatus (249,+), Pteronia glomerata (241,+), Rhus ciliata (233,+),Ruschia indurata (249,+), Salvia sp. (arp1498) (218,r), Schizoglossum aschersonianum (249,+), Selago trinervia (234,+), Senecio radicans (278,r), Senecio sp. (arp1271) (191,r), Solanum coccineum (218,r), Sutera pinnatifida (218,r), Sutera halimifolia (249,r), Sutera mollis (193,r), Sutera sp. (278,r), Tephrosia sp. (278,r), Thesium sp. (arp1326) (193,r), Unknown (arp1503)(217,r),

Appendix Table 2. The differential and companion species of the Shrublands of the Camdebo and Sneeuberg region. (a=2a, b=2b, m=2m).

Class	II																																																	
Order	A																																																	
Community number	1											2				3					4														5															
Relevé Number	83	85	91	94	97	98	99	199	271	116	117	121	122	123	243	95	96	113	114	124	84	188	189	190	197	198	200	201	244	150	195	196	238	239	129	149	167	210	222	231	232	246	247	215	130	139	143	151	159	160
Differential species of community IIA1																																																		
Grewia robusta	+		1		+				+	a	1												+												+						+									
Rhus longispina	1							1		+	1																																							
Cynodon incompletus	1							1	+		m																																							
Solanum tomentosum	+				+							r																																						
Ehretia rigida					+					+													r																											
Differential species of community IIA2																																																		
Euclea coriacea												+	+												r																									
Sutera mollis													m	m												+					r																			
Mestoklema albanicum													1					1		+																														
Aloe broomii							+					r				r																																		
Differential species of community IIA3																																																		
Diospyros austro-africana																r	+	+	+	m				+	r	+		r											r											
Elytropappas rhinocerotis															1	+	+						+						+												+									
Rhus erosa													1					a	+					r													+	1			m	+								
Crassula muscosa										+			+				r		r																													+		
Sutera halimifolia																		1																																
Selago corymbosa																			+	+																														
Olea europaea			+				m												+			r	3																											
Differential species of community IIA4																																																		
Grewia occidentalis			+					+																	r	+	+	r																						
Chenopodium phillipsianum																									r	+	+	r																						
Sporobolus fimbriatus								+																	+	+	+				+																			
Aristida congesta																									+	+			+		r	+											+							+
Indigofera heterophylla					+																				+						+	+																		
Teucrium africanum					+			+															r		r	+	+	+		+		+																		
Melica decumbens																									+	+	+																							
Solanum coccineum																r									+		+	r			r	+																		
Helichrysum cymosum																									m		b	1																						
Eragrostis chloromelas																						+		a	1	+	1	+			+												r							
Lantana rugosa																					+		r			+		+				+																		
Solanum rigidum																										+	+																							
Differential species of the community IIA5																																																		
Eragrostis curvula									+																								r		+		+	r												
Nenax microphylla														+																	+		b							+	+									
Becium burchellianum					+																															+		r				3	m	m			+	+	1	+
Melolobium candicans																																						r				r								
Tragus racemosus																																				1			+	+	+					+	+			
Helichrysum dregeanum																																									r	r	r							
Eriocephalus umbellatus															+																																	+		1

Differential species of communities IIA4 & IIA5

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Species	I	II	III	IV	V
Differential species of communities IIA4 & IIA5					
Heteropogon contortus				+ ++r1 r1r+	++ + r+ r 1r+rm1
Digitaria eriantha			r	+ 1+1+ mm11	b+r ++++
Indigofera sessilifolia				+++ + +++	+ r
Eriocephalus africanus				1m +1m1m r	1 a+
Enneapogon scoparius			+	+ 1+r	a r + 1r
Cymbopogon plurinodis			1	+ am + 11r	a+ r ++
Differential species of the communitities IIA1 IIA2, IIA3, IIA4 & IIA5					
Rhus undulata	1 a1mmar+a	+	bmm +	rmr111b	r ++
Acacia karroo	1+ 1 1++1			1+ + ++	+ +1 +
Maytenus polyacantha	m 1	+	1 r	++	m
Ehrharta calycina	+ + ++	a	+m	1m +	+
Euclea undulata	1 +		+1+		m
Euryops spathaceus	+ 1 + 3a		+++m1		3
Buddleja saligna	+ m	++	1		m m
Companion species					
Pentzia incana	4mm4aaab3+4	+	aa r	a rr+mm + ar	r + ++ 111
Chrysocoma ciliata	1 +	4b1b	1m1am	a+1r++ m +r	+ r + + +r r
Themeda triandra	m	r	ab	+ rr1bar a 3	1 1+ r m1+ ++m
Walafrida geniculata	+1 +1		+++	+ + +1 r1	r++r++
Eragrostis lehmanniana	+		11+	+ r	++r r m ++
Hibiscus pusillus	+ +		+1	++ +1+++ +++	r ++rr
Eragrostis obtusa	+		+	++ +r++1	+ ++ + +
Blepharis villosa	+		1+1	+ ++1++ ++	+ +
Tragus koeleroides	1		m	11+31m+1+++m 1	+ ++ 1
Aristida diffusa		a	1	++1 +rr	am a1a31 1+1++
Felicia filifolia		r		+ r r1	+ ++
Felicia muricata	+			+ + rm	1 +++
Lycium schizocalyx	+	+		+ r++ ++	rr r
Protaspargus suaveolens	+ +			+++ + +	r
Helichrysum rosum	+ ++	+	+	++ r	m + +1+1+
Merxmuellera disticha		+	m	r 1	3 +
Aptosimum procumbens				+ +	+ + +
Protasparagus striatus	+ + +			r +1+	
Euphorbia mauritanica				+ + +	
Eustachys paspaloides			+	1+	
Limeum aethiopicum				+	+ r
Euryops anthemoides				++	
Blepharis capensis				+ r	r +
Indigofera denudata		r	+		
Hermannia althaeoides	+ +			r +	
Sporobolus nitens			r	r	
Viscum obscurum			r	r	
Senecio radicans	+		+	+	
Pegolettia retrofrcata				+	+ +
Protasparagus subulatus		+		+	
Eustachys mutica				+ +	
Lycium oxycarpum	1				
Aloe ferox	+				
Eriocephalus ericoides	1				
Protasparagus plumossus	+				
Sarcostemma viminale	+				

Infrequent species

Alepidea capensis (130,+), Arctotis acaulis (196,+), Boerhavia cordobensis (190,r), Buddleja glomerata (84,r), Carissa haematocarpa (189,+), Chaschanum dehiscens (113,+), Cheilanthes hirta (113,+), Chenopodium phillipsianum (199,+), Commelina africana (130,r), Crassula capitella (113,r), Crassula tetragona (113,r), Dioscorea elephantipes (91,+), Diospyros lycioides (189,r), Dodonaea viscosa (155,r), Enneapogon desvauxii (149,1), Eragrostis plana (239,1), Exomis microphylla (199,+), Euryops anthemoides (271,+), Felicia hyssopifolia (113,a), Gazania linearis (155,r), Gethylis spriralis (188,r), Gnidia cuneata (113,+), Hermannia filifolia (197,r), Hyparrhenia hirta (244,+), Indigofera alternans (130,+), Lepidium africanum (190,r;196,r, 199,r), Leucas capensis (130,+), Lightfootia nodosa (244,+), Maytenus heterophylla (189,+), Othonna cylindrica (113,+), Oxalis sp. (113,+), Pentzia sphaerocephala (210,+), Phymaspermum parvifolium (190,r), Protasparagus acocksii (238,+), Protaspargus africanus (129,+), Protasparagus racemosus (113,+), Pteronia glauca (132, r), Rhus pentheri (198,r), Rosenia humulis (124,1;196,r), Solanum rigescens (199,+), Sutera pinnatifida (116,+; 190,r), Sutera atropurpurea (210,+), Talinum caffrum (150,r), Thesium namaquense (113,r), Thesium rigidum (130,+), Vepris lanceolata (167,+)

Appendix Table 3. The differential and companion species of the Grassy Dwarf Shrublands of the Katberg sandstones of the Cradock region.

Class	III	
Order	A	
Community	1	2
Relevé number	111111111111111 022333333444555 378145678012345	111111111112 9334444455691 2234567878522
Differential species of the community IIIA1		
Melolobium candicans	r+ 1	
Tragus koeleroides	++ +2 +	+2 +1
Blepharis capensis	r+	+ r+
Indigofera alternans	+++r r	+
Ehretia rigida	1 +	
Nenax microphylla	+ 1 + rr	
Limeum aethiopicum	++ +r	
Becium burchellianum	1 r++r	1 r
Tragus racemosus	+ + 11+1+1	+ + +
Helichrysum zeyheri	+ rr+	+ r
Felicia muricata	+ r +r+	
Nemesia floribunda	rr r	
Microchloa caffra	+ +	
Moraea polystachya	2 rr	
Paspalum sp.	+r	
Differential species of community IIIA2		
Rhus undulata		m + m 1
Lycium oxycarpum	a	+ +
Setaria sphacelata		+ r2 r
Sutera pinnatifida	+	r r
Blepharis villosa		+ r + r
Aptosimum procumbens		+ r r
Crassula obovata		rr rr
Differential species of communities IIIA1 & IIIA2		
Enneapogon scoparius	++++ 12r+ +r	1312+1+12 12
Aristida diffusa	1 1bb+b+++	m ama ++m
Eragrostis obtusa	+ m + rm	+++r1++
Helichrysum rosum	+ + +	r r 1+1
Chrysocoma ciliata	1 + + m	+ ++++ + ++
Heteropogon contortus	+m +	rr
Thesium hystrix	+ +1 ++	+r1 +
Indigofera sessilifolia	2 r r	+ +
Themeda triandra	1	+
Companion species		
Pentzia incana	m1a+1mbb++ +bma	ama+ma11 mbb1
Eragrostis lehmanniana	1m1 + m1+ + +bb	1++ m ++
Aristida congesta	+1 m 11+ 111	+
Protasparagus plumossus	++	++ r
Eriocephalus umbellatus	1 r	+ r
Lighfootia albens	+ 1	r
Crassula muscosa	++	r r
Lepidium africanum	++ r	
Eberlanzia spinosa	+ r	r
Fingerhuthia sesleriiformis	+	r r
Cymbopogon plurinodis	1	r +
Mesembryanthemum sp.	1 + +	
Oenothera sp.	+ r r	
Digitaria eriantha	a	r
Teucrium africanum		+r
Sporobolus nitens	r	r
Rhigozum obovatum	1	+
Eragrostis curvula	+	r
Felicia filifolia	+	+
Polygala leptophylla	+	r +
Protasparagus suaveolens		+ +
Lycium schizocalyx	+	+
Solanum tometosum	+	+
Trichodiadema sp.	+	r
Senecio ilicifolius	+	r
Walafrida geniculata		+ r

Infrequent species

Acacia karroo (146,+), Aloe ferox (148,+), Anacampseros telephiastrum (192,+),Androcymbium melanthioides (137,r), Aristida ciliata (127,+), Atriplex lindleyi (103,+), Cadaba aphylla (103,r), Chloris virgata (154,1), Convolvulus ulosepalus (127,+), Cucumis myriocarpus (127,+), Cynodon dactylon (154,+), Dicoma spinosa (162,r), Diospyros lycioides (148,r), Enneapogon desvauxii (212,+), Euphorbia mauritanica (157,r), Gnidia microphylla (212,r), Gazania sp. (arp836)(147,r), Hermannia althaeoides (165,r), Hermannia coccocarpa (136,+), Hermannia vestita (127,+), Hereroa dolabriformis (131,+), Hertia pallens (212,r), Hypertelis bowkeriana (138,+),Hibiscus aridus (145,r), Hibiscus pusillus (192,+), Kedrostis africana (103,r), Melica racemosa (92,+), Merxmuellera disticha (158,1), Mestoklema sp. (147,+), Mohria sp. (134,+), Oxalis sp. (147,r), Pachypodium succulentum (147,r), Panicum maximum (192,+),Pegolettia retrofracta (158,1), Salsola aphylla (153,r), Sarcocaulon camdeboense (148,r), Stipagrostis ciliata (127,+), Tetragonia

Appendix Table 4. The differential and companion species of the Grassy Dwarf Shrublands of the Camdebo and Sneeuberg region.

Class	III																																						
Order	B																																						
Community	1																																						
Relevé number	89	93	100	101	109	111	152	161	164	170	183	184	185	186	205	207	208	209	221	225	229	230	235	236	237	240	242	245	248	256	257	258	261	266	267	279	280	281	106	107
Differential species of the community IIIB1																																								
Eragrostis lehmanniana	1	+	1	+		r											+		+		r			+	r				m	1		r				a	+				
Eberlanzia spinosa			+		r	+			r				+	+	1		+	r							r	+		1			r		1	+				m		
Eragrostis obtusa			+	+	r	r		+	1	r					+			r		r		+			+		+		+		r	+	+		1	+	+			
Lycium schizocalyx								1			r	+	r	+	+	r			r	r	r		+	+	+	r	+	+	r	+	1		+	r	1	+		r		
Rosenia humulis			r						+	+	+	1		+						r	r	r		+		+		+	1		r	r	r	r	+					
Blepharis villosa									r			r	+	+	+	+		r						+					r		+			r	+					
Eriocephalus ericoides									a	r						+	+	1				b	1	+		b	r			r	+		r		r	+				
Galenia sarcophylla											1	+	r	+							+	+			r		r												
Protaspargus suaveolens									+						+		+	r												r				+	+				+
Mestoklema tuberosum												r					+			r					+								r	r						
Aristida diffusa														1			+						r	r			r														+	
Felicia filifolia																	+	+				r																	+		
Pegolettia retrofracta												+	r											r							r										
Thesium hystrix																	r		+								r							r				+					
Trichodiadema bulbosum											+		r										r		r																
Melica racemosa		+																					r						r														
Thesium rigidum	+												r	r																											
Helichrysum zeyheri												r			r		+																								
Sutera pinnatifida												r	+															r																
Tragus racemosus																					1			+						+												
Eragrostis chloromelas																							+						1											+			
Aptosimum procumbens																	r							r	+	+																		
Gazania linearis																													r		r	r											
Sarcocaulon camdeboense																									r					r	+		r		+					
Indigofera sessilifolia																																+	r			r					
Enneapogon scoparius																													+					r						
Microchloa caffra																																		1	m			+			
Companion species																																								
Pentzia incana	a	b	m	m	+	+	1	a	b	b	1	b	m	1	+	+		+	+	+	b	m	m	b	b	r	+	m	b	r	+	+	+		m	b	r	+	1	+
Aristida congesta	m	+	1	+	+			+	1	+					+	+	+	+	r	m		+	+	r			+	+	+	+	+	+	+	+	a	+	+	+	+	1
Chrysocoma ciliata		+			+	+		+	+	1	r			r	+	+				r	+	+	+			+	+	+			1					+				+
Felicia muricata	+		r	r			+	m		+	r	+	+	+			+	r						r	+										+		r	r	+		
Tragus koeleroides		1							m									+								+	+	a					+	+			a	+		
Senecio acutifloius									1		+																							+	+					
Hibiscus pusillus							+											+																								
Eragrostis curvula							r																					r		+										r	+		
Digitaria eriantha																	+					b																	+		
Merxmuellera disticha							a																		r			+														
Nenax microphylla																	+									r													+			
Helichrysum dregeanum																													r		r												
Helichrysum rosum												+																												+
Hermannia cuneifolia																	+																					+		
Euphorbia ferox																								r									r							
Cynodon incompletus															+		+										+						+								
Lepidium africanum										r	r										+													r		r			
Atriplex semibaccata								+														r																		
Limeum aethiopicum																									r											+					
Walafrida geniculata								+														1						1									1				
Amaryllis sp.			+	+																																				
Protasparagus acocksii									r					r																										
Crassula muscosa										+				+																											
Chloris virgata				+				+																																
Anacampseros telephiastrum									+		+																												
Lightfootia albens														+		+																								
Euphorbia mauritanica																	+					r																		
Acacia karroo																+					r																		
Protaspargus striatus																									+										+					

Infrequent species

Boerhavia cordobensis (106,r), Becium burchellianum (205,r), Blepharis capensis (207,r), Boophane disticha (281,r), Bulbine abyssinica (266,r), Bulbine frutescens (186,r), Commelina africana (237,1), Crassula corallina (185,r), Crassula capitella (235,r), Cynodon dactylon (161,+), Delosperma aliwalense (237,r), Delosperma parvifolium (237,r), Dianthus namaensis (185,+), Drosanthemum lique (237,r), Drosanthemum obliquum (281,m), Euphorbia clavarioides (235,+), Euphorbia gorgonis (281,1), Euphorbia valida (281,r), Elytropappus rhinocerostis (235,r), Fingerhuthia sesleriiformis (248,r), Geigeria ornativa (186,+), Gethylis spiralis (225,r), Grewia occidentalis (152,+), Helichrysum bolusianum (186,r), Hermannia linearifolia (248,+), Lycium oxycarpum (152,+), Monechma spartioides (185,r), Moraea polystachya (161,r), Mestoklema illepidum (236,r), Melolobium candicans (261,r), Osteospermum calendulaceum (230,+), Pachypodium succulentum (261,r), Pentzia quinquefida (208,+), Pentzia globosa (170,1), Plinthus karooicus (248,+), Psilocaulon articulatum (248,1), Pteronia glauca (240,1), Rhigozum obovatum (261,+), Sarcostemma viminale (261,r), Schismus inermis (248,+), Selago trinervia (230,r), Sporobolus fimbriatus (230,r), Zygophyllum gilfillani (106,r),

Appendix Table 5. The differential and companion species of the Dwarf Shrubland *typicum* of the Camdebo.

Class	III													
Order	C													
Community	1													
Relevé number	1	1	1	1	1	2	2	2	2	2	2	2	1	1
	1	5	6	6	6	0	1	1	1	1	2	2	7	7
	2	6	2	3	8	6	1	4	5	6	6	8	1	2
Differential species of community IIC1														
Rhigozum obovatum	m		b	a	m									
Pachypodium succulentum	r		+	+	r									
Haworthia viscosa	1		1											
Sutera halimifolia	1		m	1										
Polygala hottentotta	+		+											
Blepharis capensis	+		+	1										
Pteronia glauca			r	+										
Euryops anthemoides				1	1				+					
Indigofera sessilifolia						r			+					
Walafrida geniculata						r		+	+					
Nenax microphylla						r	+							
Sporobolus ludwigii							r	r						
Eragrostis curvula							a	+	r	+				
Gnidia microphylla									+	+	r			
Merxmuellera disticha								1		+				
Pentzia globosa							r			+				
Lycium schizocalyx							r	+		+				
Bulbine abyssinica			+									r		r
Geigeria ornativa													+	+
Mesembryanthemum karrooense													m	+
Ornithogalum sp													+	+
Lepidium africanum													+	+
Blepharis villosa	1		+	1		+					+	r		r
Crassula muscosa	+		+	r									+	+
Senecio radicans	+		1	+	r				+					
Eberlanzia spinosa		r				r			1			r	m	1
Trichodiadema setuliferum			+	+							r			
Companion species														
Pentzia incana	1	+	1	+	m	+	+	+	+	+	+	+		r
Aristida congesta	1	1	m	m	m	+	m	m	m	m	1	1		
Eragrostis lehmanniana	1	3	b	+		+	1	1		1	+	+		
Eragrostis obtusa		+	+			+	+		+	+		+		
Protaspargus suaveolens	+		1	+		+			r		r			
Chrysocoma ciliata		+	1	+	r	+						+		+
Rosenia humulis			m	m			+						r	+
Aristida diffusa	1			+		m				1	r			
Aptosimum procumbens	+		r		r				+					
Tragus koeleroides	m		b	1		1	1							
Eriocephalus ericoides			+	m				m						
Felicia filifolia	+					+	+							
Tragus racemosus					m				+			+		
Thesium rigidum			+								+			
Pegolettia retrofracta	+			+										
Helichrysum rosum			r			r								
Cadaba aphylla	+							r						

Infrequent species

Anacampseros telephiastrum (163,+), Barleria obtusa (168,+), Becium burchellianum (206,r), Chloris virgata (211,+), Cuspidia cernua (171,1), Cynodon incompletus (172,m), Dianthus namaensis (171,+), Digitaria eriantha (214,+), Ehrharta calycina (214,r), Elytropappus rhinocerotis (214,+), Eragrostis bergiana (216,+), Eragrostis bicolor (211,r), Eriocephalus africanus (168,1), Euphorbia mauritanica (162,+), Faucaria tigrina (112,+), Felicia hyssopifolia (163,1), Haworthia deltoidea (163,m), Hermannia filifolia (206,r), Helichrysum dregeanum (215,+),Hermannia cuneifolia (214,r), Indigofera denudata (112,1), Justicia cuneata (112,r), Lightfootia albens (214,r), Melolobium microphyllum (216,+), Melolobium candicans (228,r), Melica racemosa (211,r), Mestoklema tuberosum (206,r), Moraea polystachya (156,+), Protasparagus acocksii (163,+), Salsola aphylla (214,r), Salvia repens (172,+), Solanum tomemtosum (156,r), Sutera mollis (162,+), Sutera pinnatifida (112,1), Tetrachne dregei (214,r), Tribulus terrestris (228,r), Thesium hystrix (206,+), Zygophyllum incrustatum (211,r),

Appendix Table 6. The differential and companion species of the Succulent Dwarf Shrublands of the Camdebo plain.

Class	III										
Order	D										
Community	1										
Relevé number	1	1	1	1	2	2	2	1	1	1	1
	7	7	7	7	5	5	6	7	7	6	8
	5	6	7	8	3	9	3	3	4	9	7
Differential species of community IIID1											
Senecio longiflorus	r	r		r		r		r			
Senecio acutifolius	r	1	r	r	r	r			r		
Haworthia viscosa	r	+	+	1		+					
Trichodiadema pygmaeum	+		+	+				+	+	+	
Sarcocaulon camdeboense	r	m	r		r	r	r		r		
Rhigozum obovatum	+	1	a	a	1	+	+				
Eberlanzia spinosa	m	a	+					1			
Pachypodium succulentum	r		r	r			r	r	r		
Bulbine sp	+	+						+	+		
Blepharis villosa	+		r	r							
Bulbine abyssinica		+		+							
Crassula muscosa		r	+	r						r	
Crassula tetragona		r	r								
Senecio radicans		r	r	+		r					
Mestoklema tuberosum		+			r			m			r
Protasparagus striatus	+			+	+				+		
Euphorbia ferox			r	r	r	r					
Anacampseros telephiastrum				r							
Ruschia grisea				+							
Euphorbia esculenta					+		r				
Galenia sarcophylla			+					+	+		
Zygophyllum retrofractum								m	m		
Crassula corallina								+	r		
Crassula ericoides										r	
Salsola aphylla										a	+
Psilocaulon absimile										m	
Companion species											
Pentzia incana	m	+	1	+	a	+	+	m	1	m	m
Aristida congesta	+	+	1	1	+			+	r	+	
Lycium schizocalyx	r	1	+			+	+	+	+		1
Eriocephalus ericoides	a				1		+				
Rosenia humulis	r		+	r	r						
Thesium rigidum	+	r						r			r
Pegolettia retrofracta	r			+					a		
Eragrostis obtusa					+					r	+
Aristida diffusa				1	+	+					
Felicia filifolia				+					r		
Protaspargus suaveolens			r						r		
Tragus koeleroides					+	+					

Infrequent species

Androcymbium melanthioides (174,+), Aptosimum depressum (175,r), Cadaba aphylla (176,+), Carissa haematocarpa (253,r), Diospyros lycioides (253,r), Euphorbia mauritanica (259,+), Felicia muricata (169,+), Gazania linearis (174,+), Geigeria filifolia (177,r), Helichrysum rosum (178,r), Lachenalia bowkeri (187,r), Lightfootia albens (259,r), Limeum aethiopicum (175,r), Pteronia glauca (253,r), Rhoichissus tridentata (253,r), Senecio laevigatus (169,+), Setaria sphacelata (253,r), Sarcostemma viminale (178,r), Thesium hystrix (174,r),

Appendix Table 7. The differential and companion species of the Succulent Thicket of the Camdebo and Sneeuberg.

Class	IV																											
Order	A																											
Community	1										2													3				
Relevé number		2	2	2	1	1	1	2	2					1	1	2	1	2	2	2	2	2	2	1	1	1	1	2
	8	1	5	6	0	1	6	5	6	8	8	8	9	0	1	5	0	5	5	2	6	6	7	7	8	8	8	6
	1	3	2	9	4	9	6	5	4	2	7	8	0	2	8	1	5	0	4	7	0	2	7	9	0	1	2	5
Differential species of community IVA1																												
Rhoicissus tridentata	+	+	+							+	+							+										+
Lycium oxycarpum	+	1	+			+		+	1										+					+				+
Euclea undulata	m	+				1	a									+												
Rhus refracta	+										1	+																
Rhus longispina		m	+		+	+							1							+								
Panicum maximum			+			+	+			+							1											
Acacia karroo			+		+	1		+	1				+			+	+											
Abutilon sonneratianum			+			+																						
Schotia afra			1									+						+										+
Cussonia spicata			+									+																
Grewia occidentalis				1		+									+													
Diospyros austro-africana						1								+	+													
Viscum obscurum							+						+															
Crassula perforata			+											+		+												
Differential species of community IVA2																												
Aristida diffusa														+					+		+		+					
Diospyros lycioides																+			+	+	+	+						
Protaspargus suaveolens	+							+								+				+	+	+						
Enneapogon scoparius																			+				a					
Blepharis villosa																				r	+							
Nymania capensis																		+										
Cenchrus ciliaris																		b					3					
Differential species of community IVA3																												
Pachypodium succulentum							+														+	+			+			
Senecio longiflorus																					+	+		+	1	+	+	
Lycium schizocalyx																						+		b	1		+	+
Peliostomum origanoides										+			+	+										+	+	+	+	
Aizoon rigidum													+											+	+	+	+	
Aloe striata																								+	+	m	+	
Galenia sarcophylla																								1	+			
Euphorbia heptagona																									+	+		
Differential species of communities IVB1, 2 & 3																												
Portulacaria afra	4	3	4	3		a				a	m	a	m	m	3			+						+	3	m	4	+
Pappea capensis		+	+		1	1			1	+	+	+		+	1	+			+	+		+				1	+	
Maytenus polyacantha				m	1	+	1	m	1	m	1	+		1			+	+	+	+	+	+		+				+
Rhigozum obovatum			+			+				1	m		1		m		+	+	+	+	+	+		m	m	a	m	m
Carissa haematocarpa		+			+	+	1	+			+	+							+	+		+						
Aristida congesta								+		+	1	+	+			+			+	+	+		+					+
Boscia oleoides									1									+			+	+						
Protasparagus striatus										+				+	+			+			+	+	1	+	+			
Crassula ovata										1					+	+									+			
Aloe ferox						+						+	+	+					+	r	+	+						+

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Companion species

Pentzia incana	+ mm 1 1	mmam b ++1++1	m+++
Grewia robusta	+ mml 1	a1 1a+++ ++++	1m11+
Eragrostis obtusa	11 +	+ +1+ +	
Chrysocoma ciliata	+ 1 3	+	
Cynodon incompletus	+ 1	+ mm	
Crassula muscosa	+	++	++
Eriocephalus ericoides	+	+	
Tragus koeleroides		1 +	
Felicia muricata		+ +	
Eragrostis lehmanniana	+	+ 1	
Lepidium africanum		+	
Teucrium africanum	+	+	
Indigofera heterophylla		++	
Solanum tomentosum	+	+	
Protasparagus subulatus	+	+	
Ehretia rigida	+	+ +	
Protasparagus plumossus	+		
Sarcostemma viminale	+		
Senecio radicans		+	
Cadaba aphylla		+ +	
Limeum aethiopicum		+ +	+
Blepharis capensis		+ r+	+ +
Indigofera sessilifolia		+	+
Protasparagus acocksii		+	+
Euphorbia coerulescens		m	b
Maytenus capitata	+	+	
Becium burchellianum		+	
Rhus undulata	+	+	
Hermannia althaeoides	+		
Walafrida geniculata	+		+
Euryops spathaceus	+		
Helichrysum rosum		+	

Infrequent species

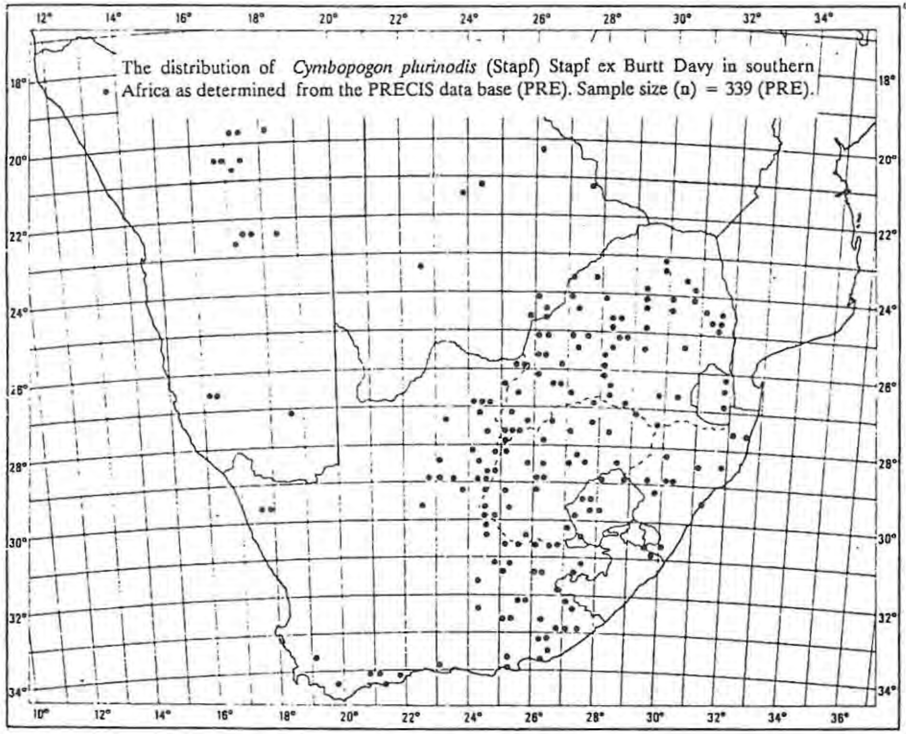
Aloe speciosa (251,+), A. arborescens (119,+), Atriplex semibaccata (179,+), Cissampelos capensis (102,+), Crassula capitella (87,+), C. falcatus (166,+), C. tetragona (251,+), C. cultrata (251,1), Cymbopogon plurinodis (102,+), Eragrostis chloromelas (269,+), Euphorbia gorgonis (213,m), E. tetragona (252,+), E. mauritanica (251,+), E. ferox (254,+), E. esculenta (265,+), Fingerhuthia sesleriiformis (260,+), Gnidia cuneata (119, +), Heteropogon contortus (105,+), Lantana rugosa (90,+), Leucas capensis (251,+), Othonna cylindrica (90,+), Panicum deustum (250,+), Pelargonium zonale (82,+), Plumbago auriculata (213,+), Protasparagus africanus (213,+), Rosenia humulis (265,+), Ruellia cordata (250,+), Rhus glauca (118,+), Sansevieria aethiopica (166,+), Sarcocaulon camdeboense (260,+), Setaria lindenbergiana (181,+), Sporobolus nitens (90,1), Stachys rugosa (81,r), Solanum coccineum (213,+), Sutera halimifolia (105,+), Thesium rigidum (104,+), Trichodiadema pygmaeum (227,+), Zygophyllum retrofractum (260,+).

Appendix Table 8. The differential companion species of the Riparian Thicket of the Camdebo.

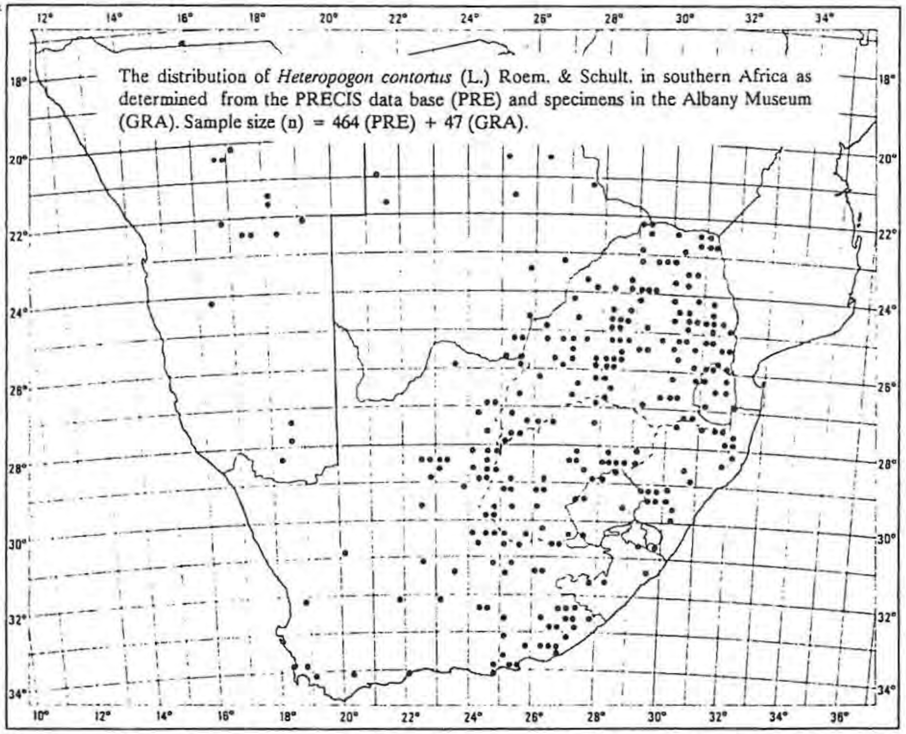
Class	V				
Order	A				
Community	1				
Relevé number		1	1	2	2
	8	1	2	2	7
	6	0	0	4	6
Differential species of the Riparian Thicket					
Ehretia rigida	r				r
Rhus pentherii	+				
Grewia occidentalis			r		+
Grewia robusta			+		+
Melolobium candicans			+		
Eragrostis lehmanniana			a		
Chloris virgata				+	
Ziziphus mucronata					+
Diospyros lycioides					+
Maytenus heterophylla					a
Azima tetracantha					r
Cussonia spicata					r
Walafrida geniculata					+
Olea europaea					m
Companion species					
Cynodon incompletus	m	m	a	r	1
Acacia karroo	1	m		r	3
Protasparagus striatus	+			+	r
Pentzia incana	+		4	+	
Aristida congesta			m	+	
Tribulus terrestris			1	+	
Atriplex lindyeii		+		+	
Infrequent species					
Lycium oxycarpum			1		
Euclea undulata					+
Lepidium africanum			+		
Lycium schizocalyx				r	
Blepharis capensis			+		
Walafrida geniculata					+
Indigofera denudata			+		
Eragrostis obtusa				+	
Pappea capensis					r
Rhus longispina					+
Boscia oleoides			1		
Juncus effusus		+			
Salsola kali	+				
Pachypodium succulentum	r				
Senecio burchelli		+			
Melolobium candicans			+		
Crassula muscosa			+		
Salsola aphylla				+	
Barleria obtusa				+	
Circium vulgare		1			

Appendix Maps

1. Distribution maps of sixty eight differential species in the Karoo Nature Reserve. Prepared from records in the National Herbarium (PRE) and the Albany Museum Herbarium (GRA). The scale appears on the first map. Arranged according to Gibbs Russell *et al.* (1984).

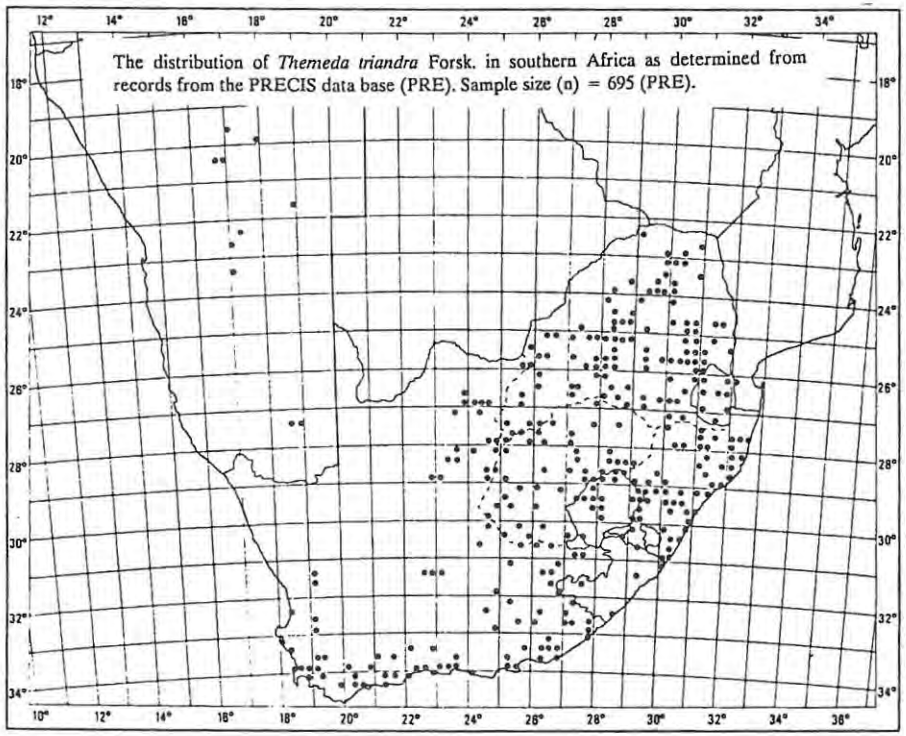


The distribution of *Cymbopogon plurinodis* (Stapf) Stapf ex Burtt Davy in southern Africa as determined from the PRECIS data base (PRE). Sample size (n) = 339 (PRE).

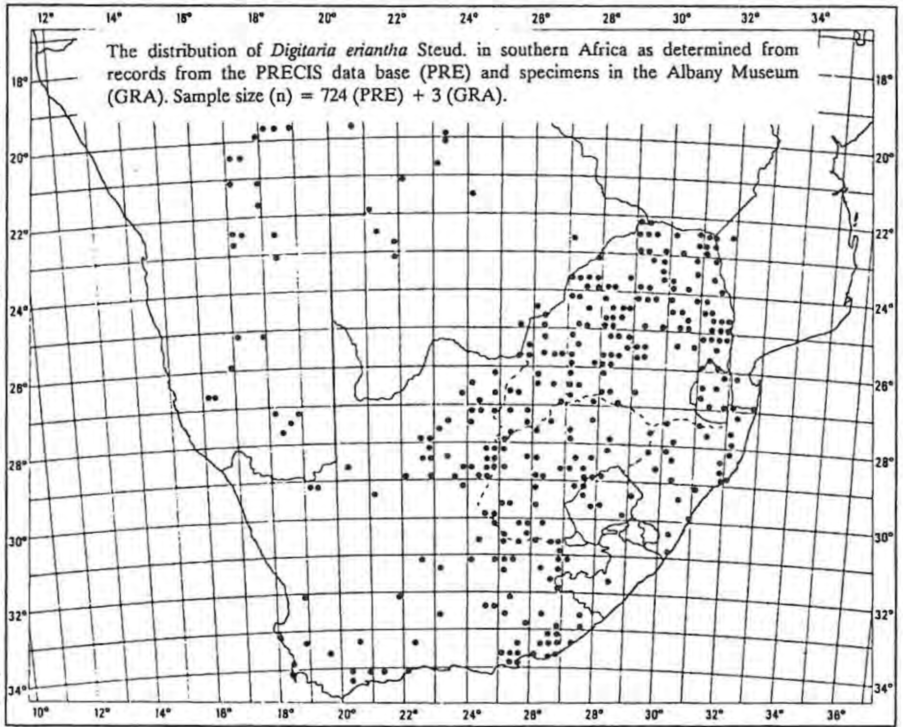


The distribution of *Heteropogon contortus* (L.) Roem. & Schult. in southern Africa as determined from the PRECIS data base (PRE) and specimens in the Albany Museum (GRA). Sample size (n) = 464 (PRE) + 47 (GRA).

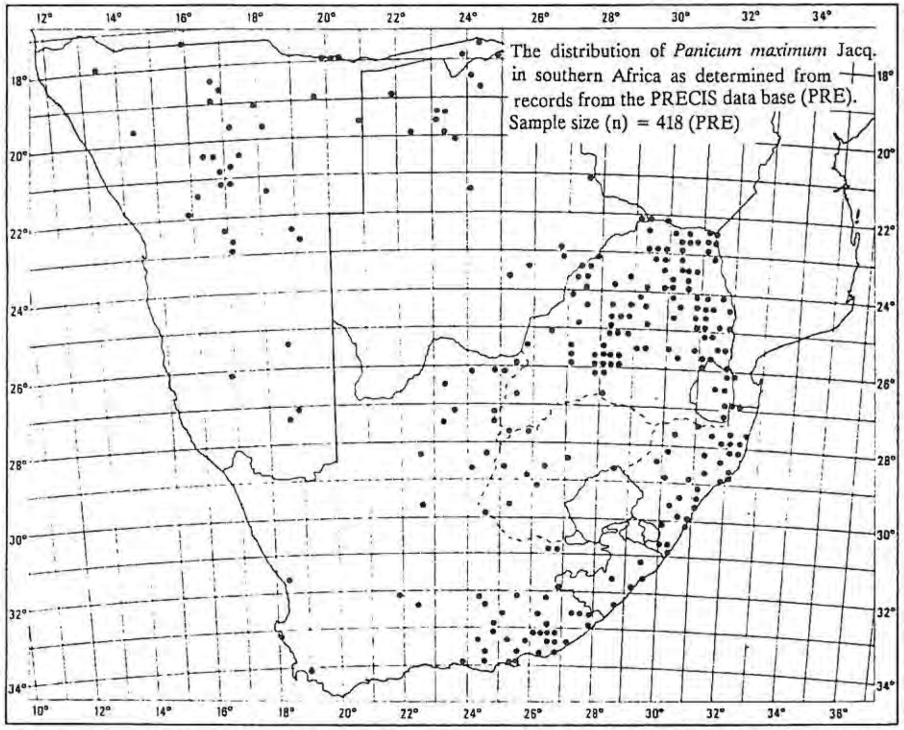
km 100 0 100 200 300 400 500 600 700 800 km



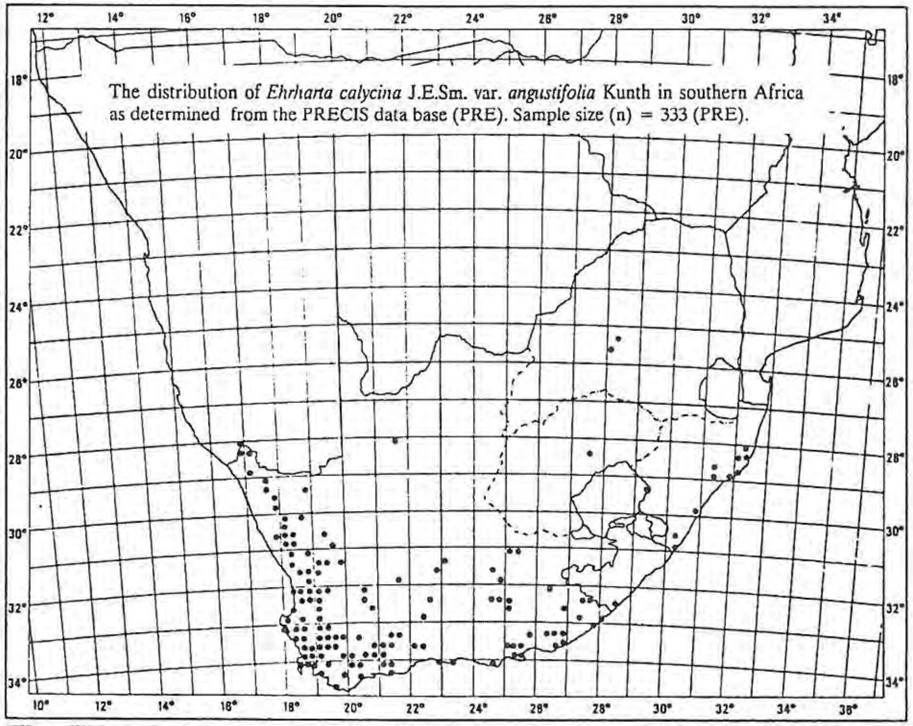
The distribution of *Themeda triandra* Forsk. in southern Africa as determined from records from the PRECIS data base (PRE). Sample size (n) = 695 (PRE).



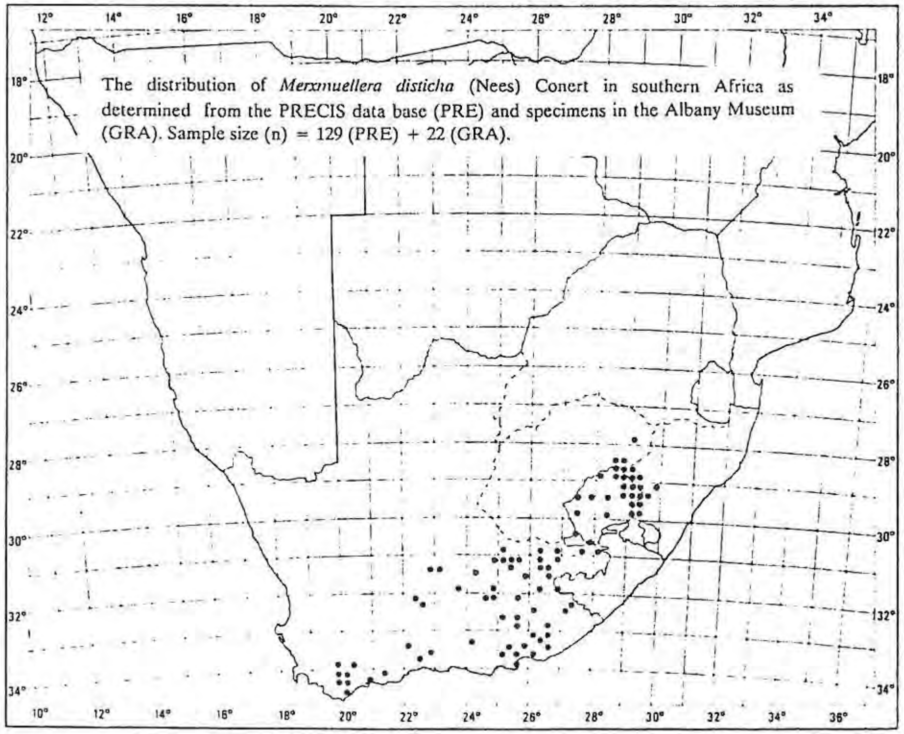
The distribution of *Digitaria eriantha* Steud. in southern Africa as determined from records from the PRECIS data base (PRE) and specimens in the Albany Museum (GRA). Sample size (n) = 724 (PRE) + 3 (GRA).



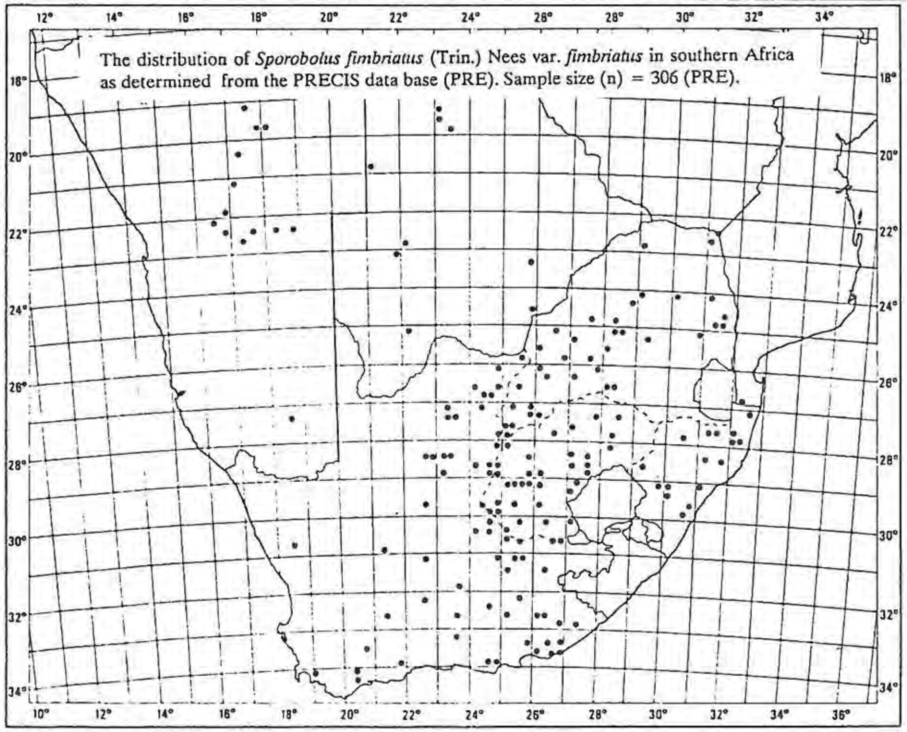
The distribution of *Panicum maximum* Jacq. in southern Africa as determined from records from the PRECIS data base (PRE). Sample size (n) = 418 (PRE)



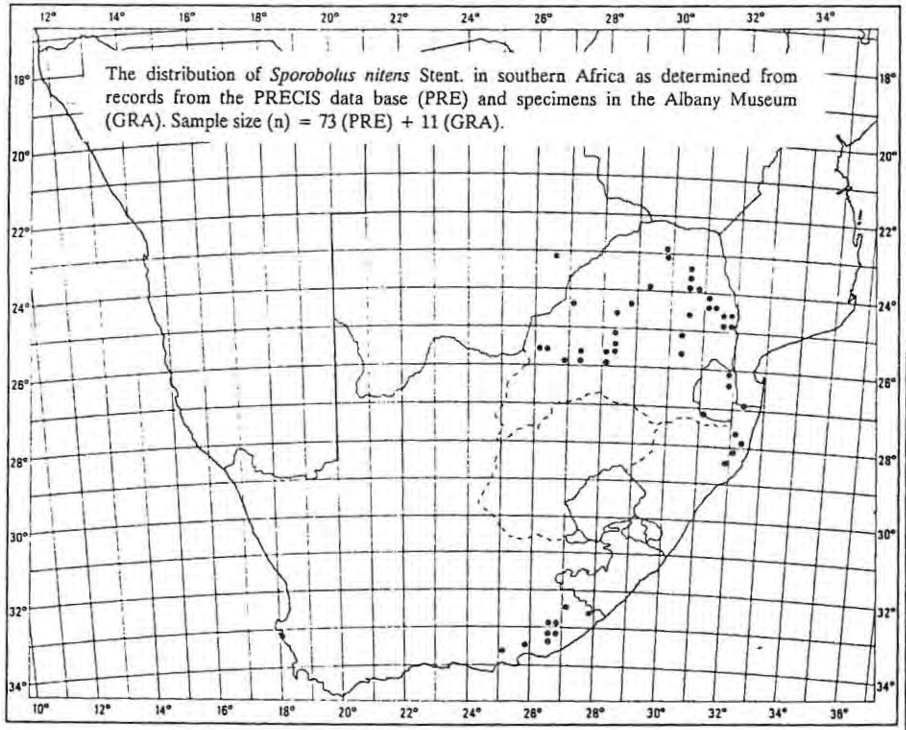
The distribution of *Ehrharta calycina* J.E.Sm. var. *angustifolia* Kunth in southern Africa as determined from the PRECIS data base (PRE). Sample size (n) = 333 (PRE).



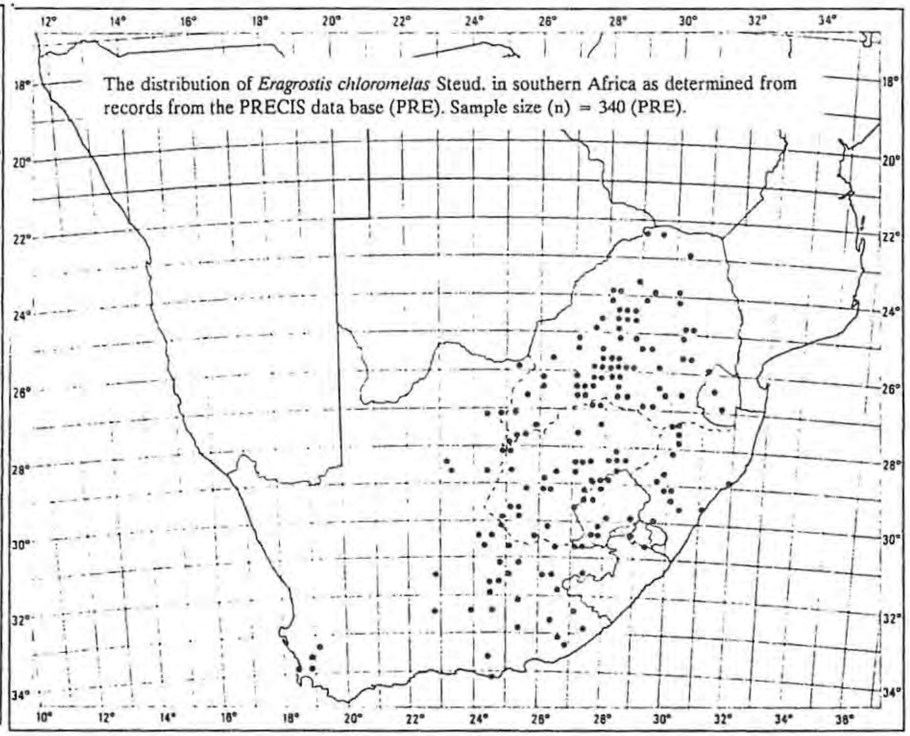
The distribution of *Merxmuellera disticha* (Nees) Conert in southern Africa as determined from the PRECIS data base (PRE) and specimens in the Albany Museum (GRA). Sample size (n) = 129 (PRE) + 22 (GRA).



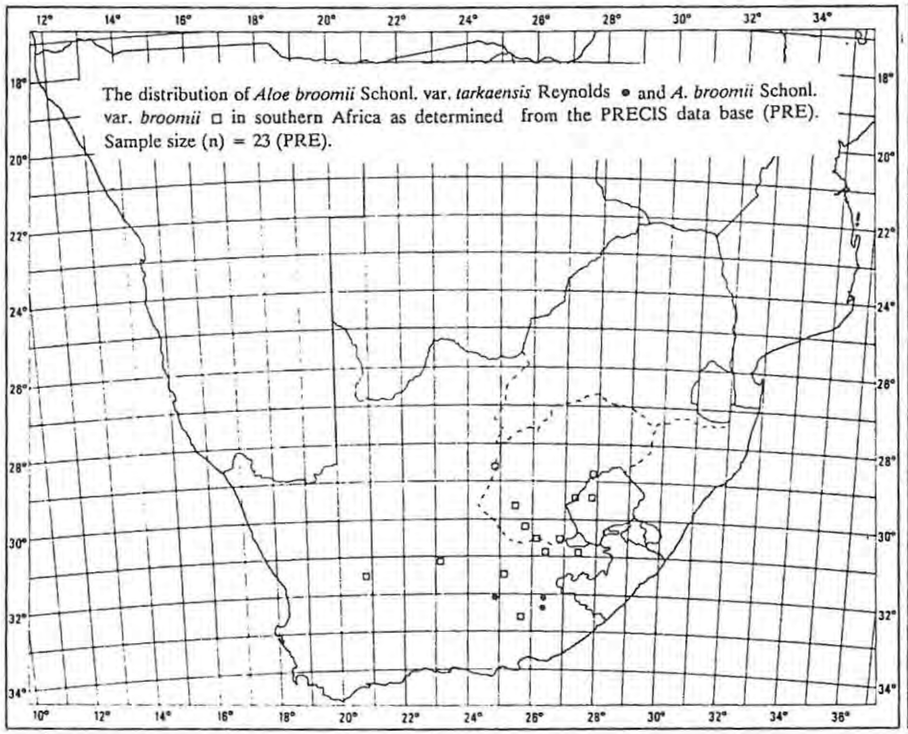
The distribution of *Sporobolus fimbriatus* (Trin.) Nees var. *fimbriatus* in southern Africa as determined from the PRECIS data base (PRE). Sample size (n) = 306 (PRE).



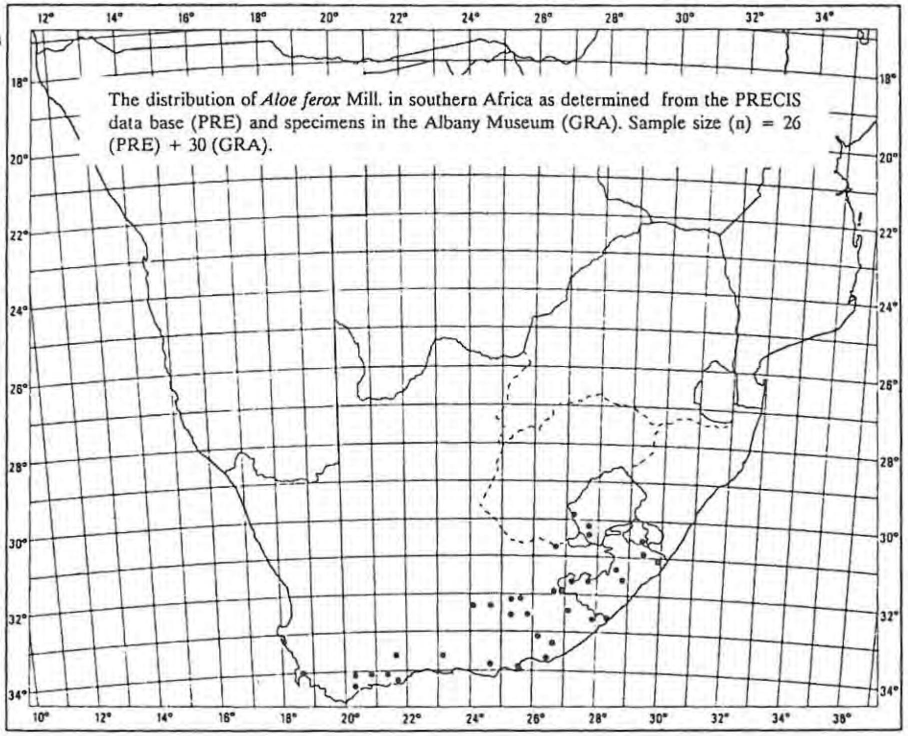
The distribution of *Sporobolus nitens* Stent. in southern Africa as determined from records from the PRECIS data base (PRE) and specimens in the Albany Museum (GRA). Sample size (n) = 73 (PRE) + 11 (GRA).



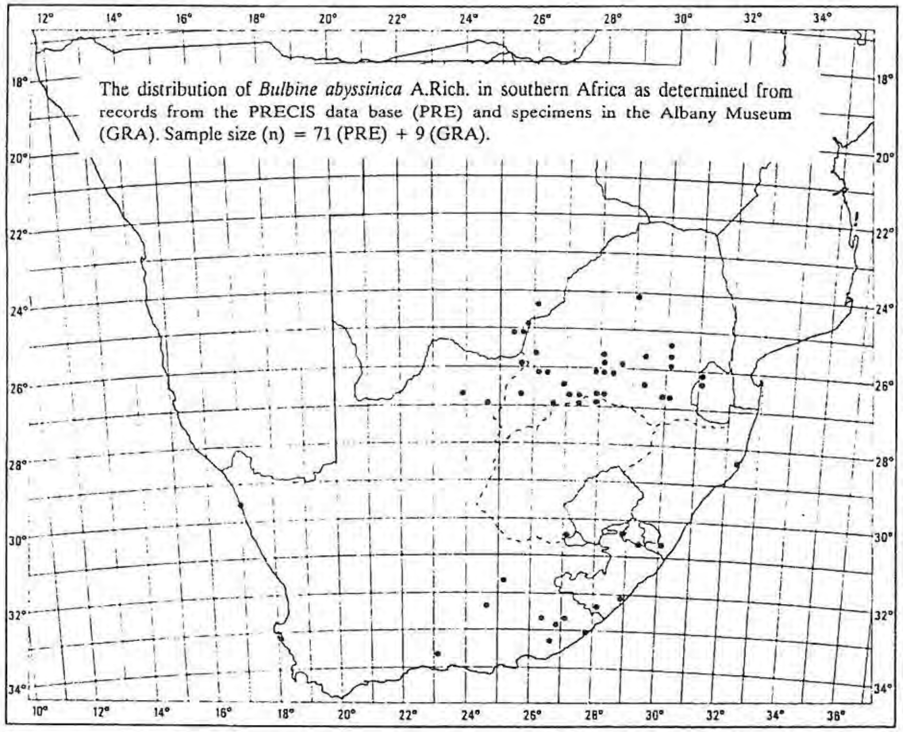
The distribution of *Eragrostis chloromelas* Steud. in southern Africa as determined from records from the PRECIS data base (PRE). Sample size (n) = 340 (PRE).



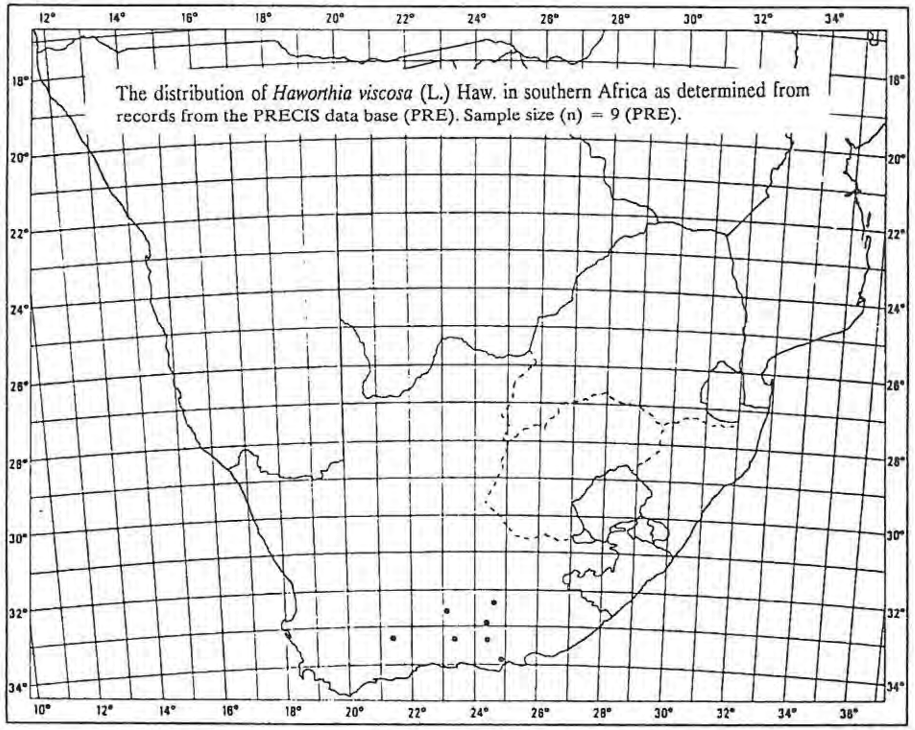
The distribution of *Aloe broomii* Schonl. var. *tarkaensis* Reynolds • and *A. broomii* Schonl. var. *broomii* □ in southern Africa as determined from the PRECIS data base (PRE). Sample size (n) = 23 (PRE).



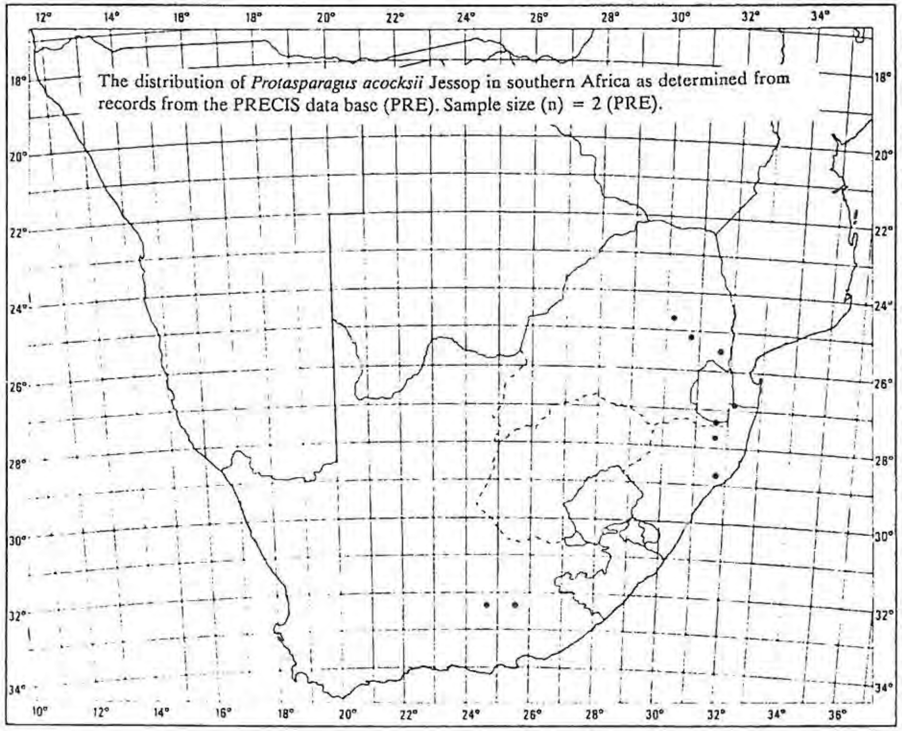
The distribution of *Aloe ferox* Mill. in southern Africa as determined from the PRECIS data base (PRE) and specimens in the Albany Museum (GRA). Sample size (n) = 26 (PRE) + 30 (GRA).



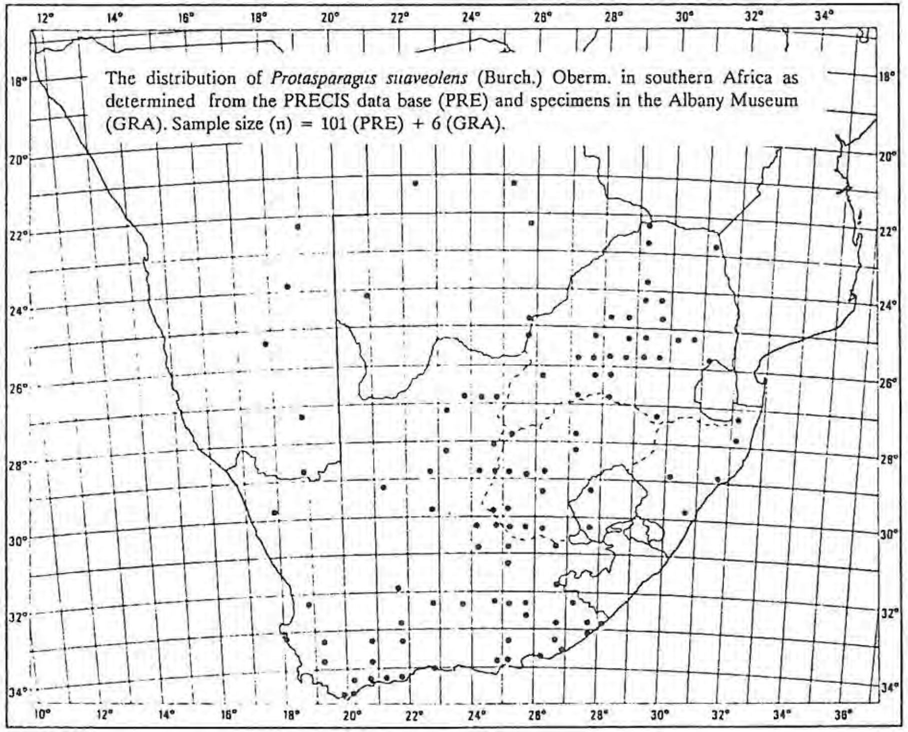
The distribution of *Bulbine abyssinica* A.Rich. in southern Africa as determined from records from the PRECIS data base (PRE) and specimens in the Albany Museum (GRA). Sample size (n) = 71 (PRE) + 9 (GRA).



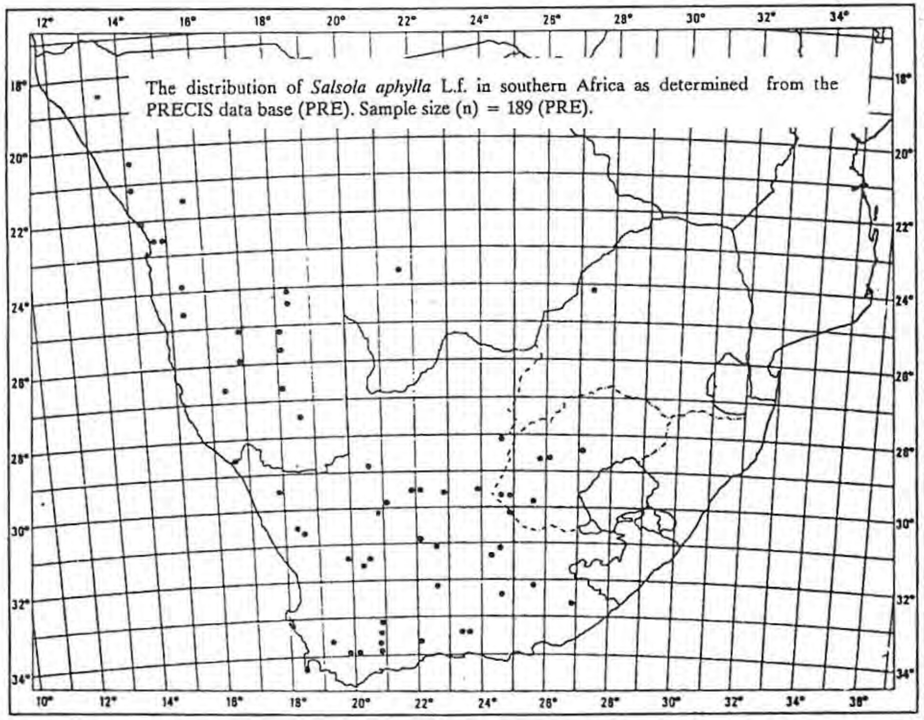
The distribution of *Haworthia viscosa* (L.) Haw. in southern Africa as determined from records from the PRECIS data base (PRE). Sample size (n) = 9 (PRE).



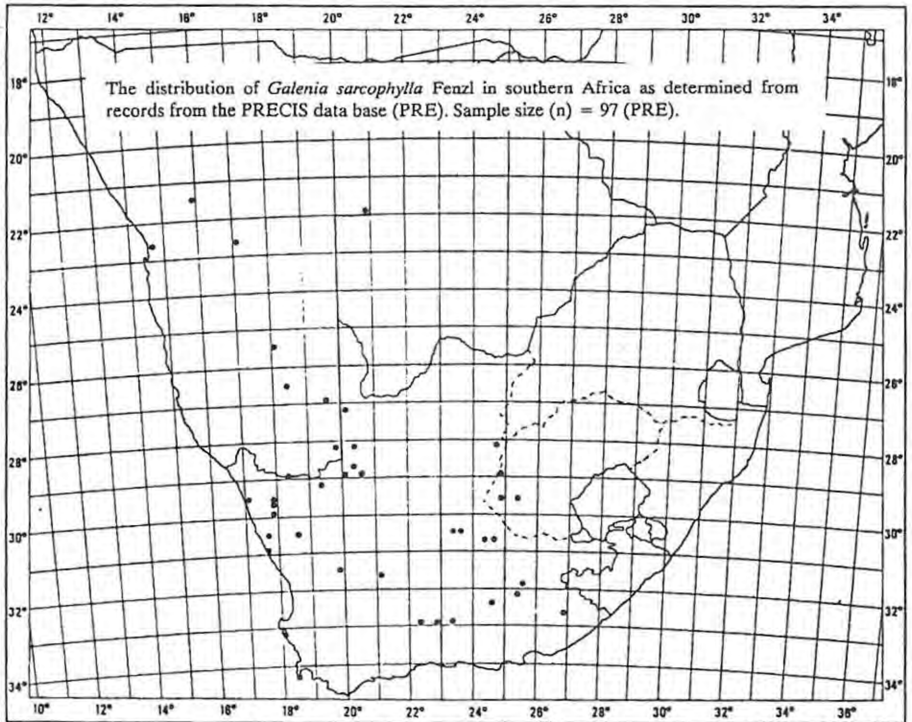
The distribution of *Protasparagus acocksii* Jessop in southern Africa as determined from records from the PRECIS data base (PRE). Sample size (n) = 2 (PRE).



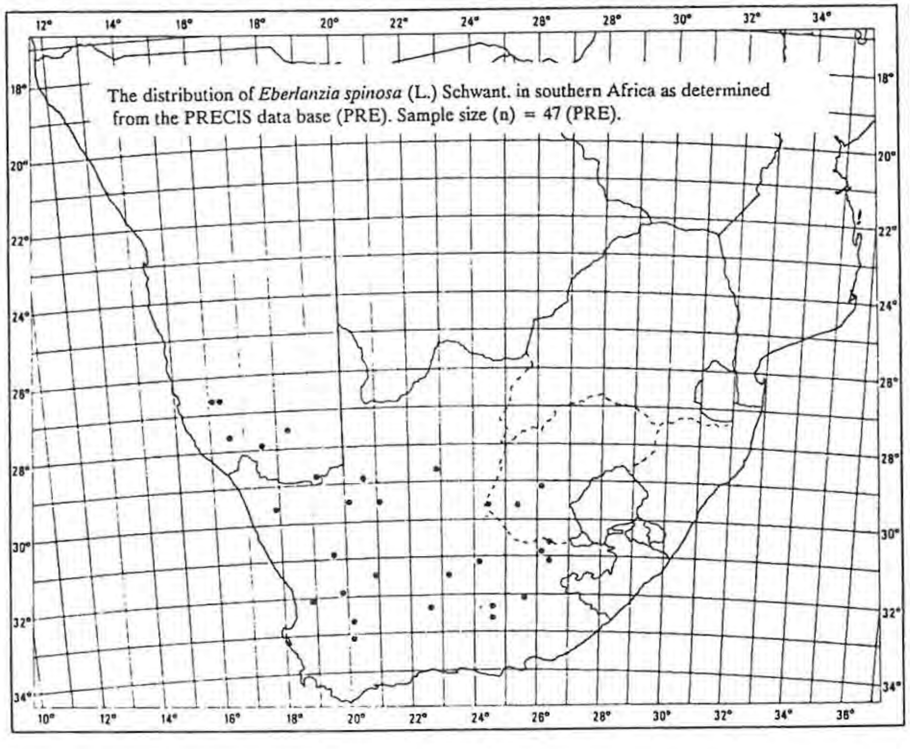
The distribution of *Protasparagus suaveolens* (Burch.) Oberm. in southern Africa as determined from the PRECIS data base (PRE) and specimens in the Albany Museum (GRA). Sample size (n) = 101 (PRE) + 6 (GRA).



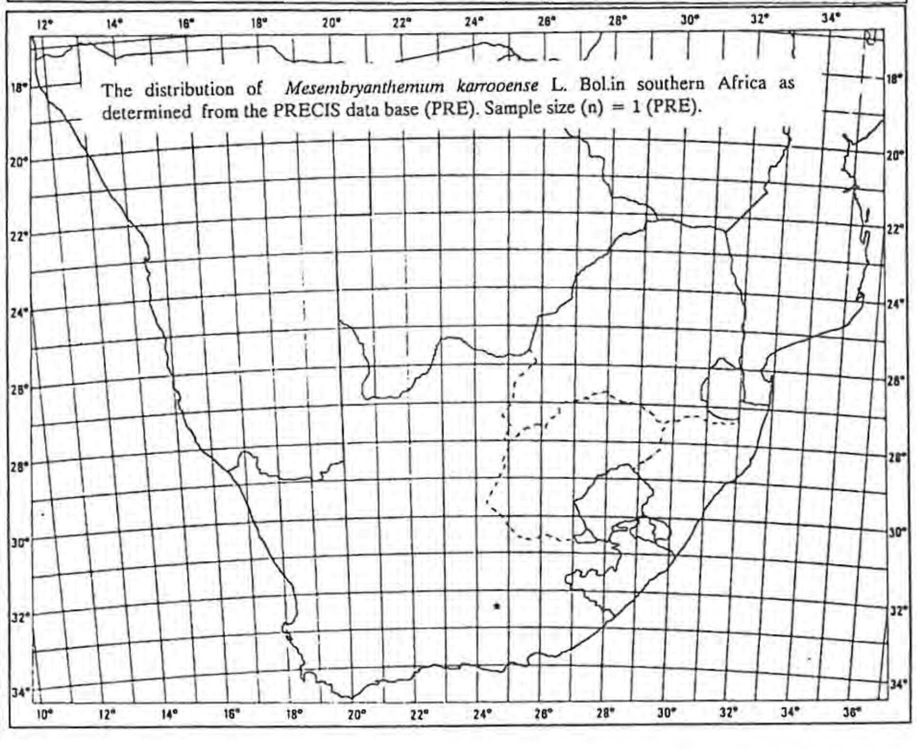
The distribution of *Salsola aphylla* L.f. in southern Africa as determined from the PRECIS data base (PRE). Sample size (n) = 189 (PRE).



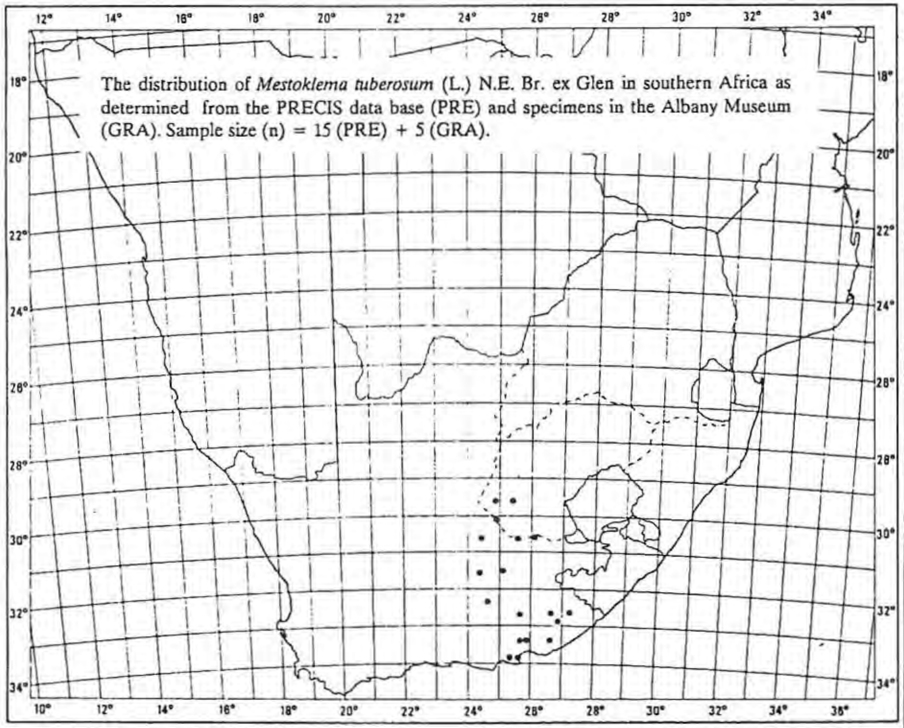
The distribution of *Galenia sarcophylla* Fenzl in southern Africa as determined from records from the PRECIS data base (PRE). Sample size (n) = 97 (PRE).



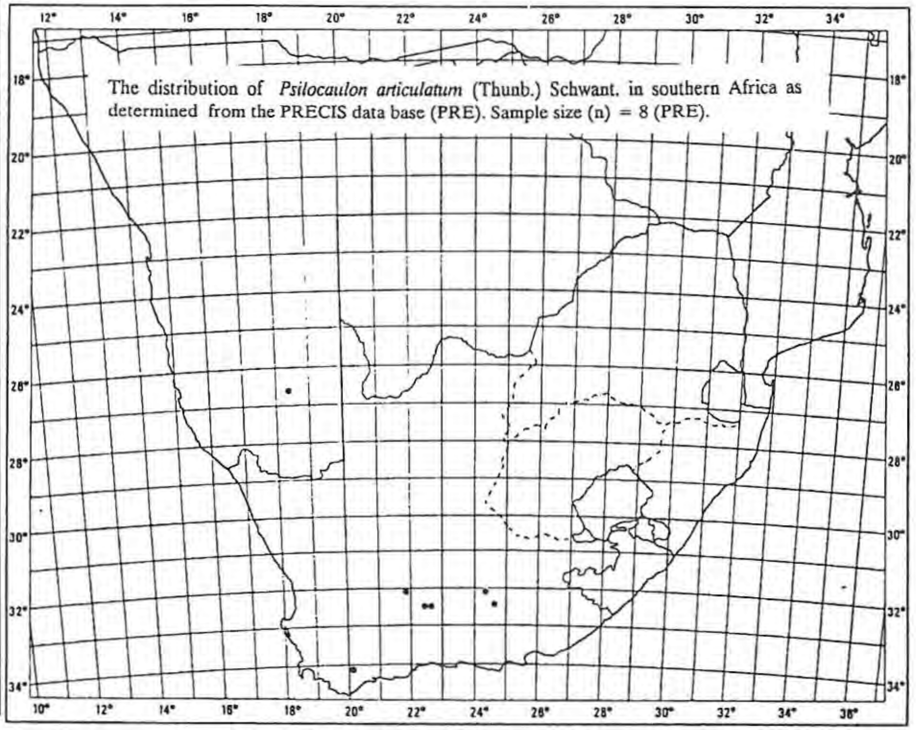
The distribution of *Eberlanzia spinosa* (L.) Schwant. in southern Africa as determined from the PRECIS data base (PRE). Sample size (n) = 47 (PRE).



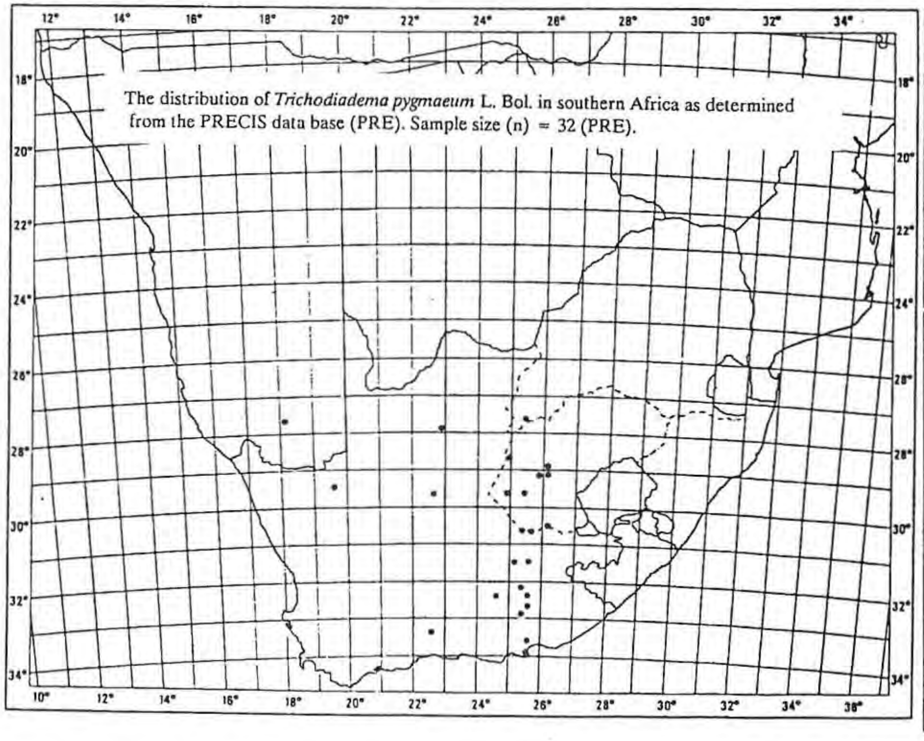
The distribution of *Mesembryanthemum karrooense* L. Bol.in southern Africa as determined from the PRECIS data base (PRE). Sample size (n) = 1 (PRE).



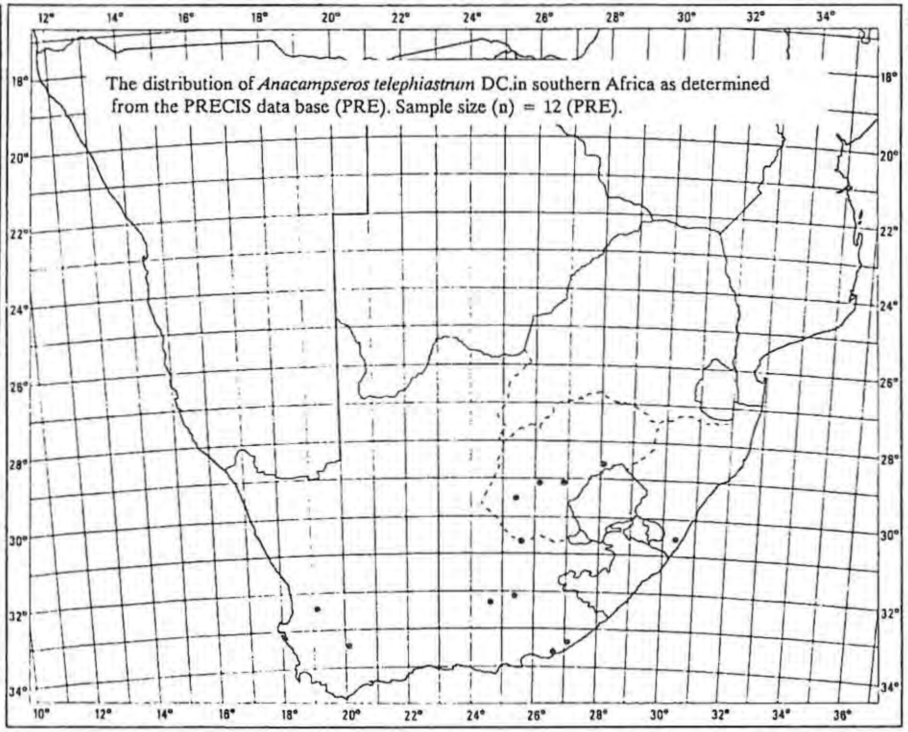
The distribution of *Mestoklema tuberosum* (L.) N.E. Br. ex Glen in southern Africa as determined from the PRECIS data base (PRE) and specimens in the Albany Museum (GRA). Sample size (n) = 15 (PRE) + 5 (GRA).



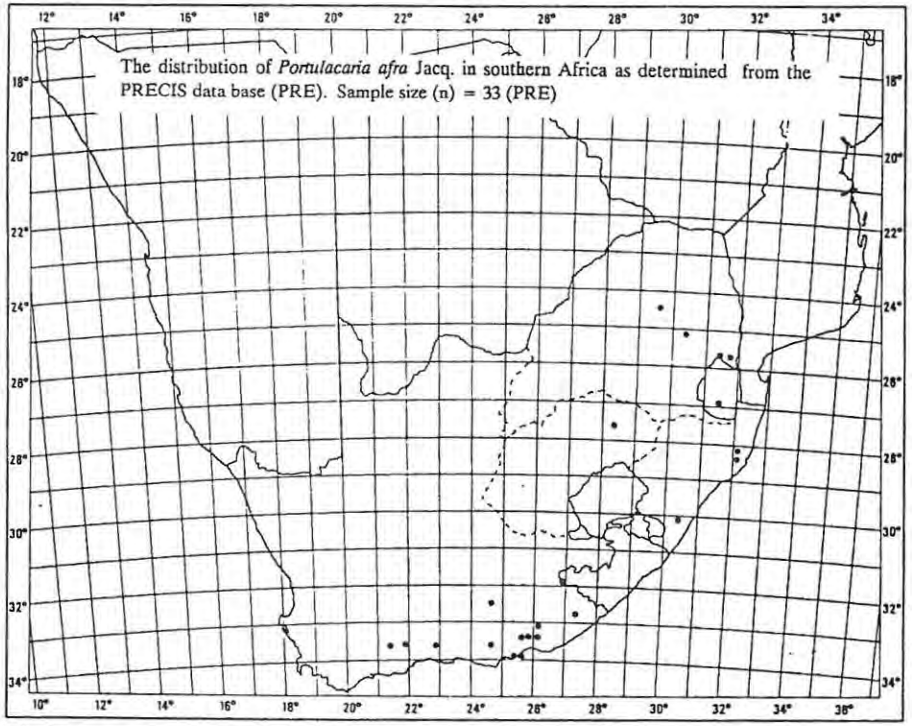
The distribution of *Psilocaulon articulatum* (Thunb.) Schwant. in southern Africa as determined from the PRECIS data base (PRE). Sample size (n) = 8 (PRE).



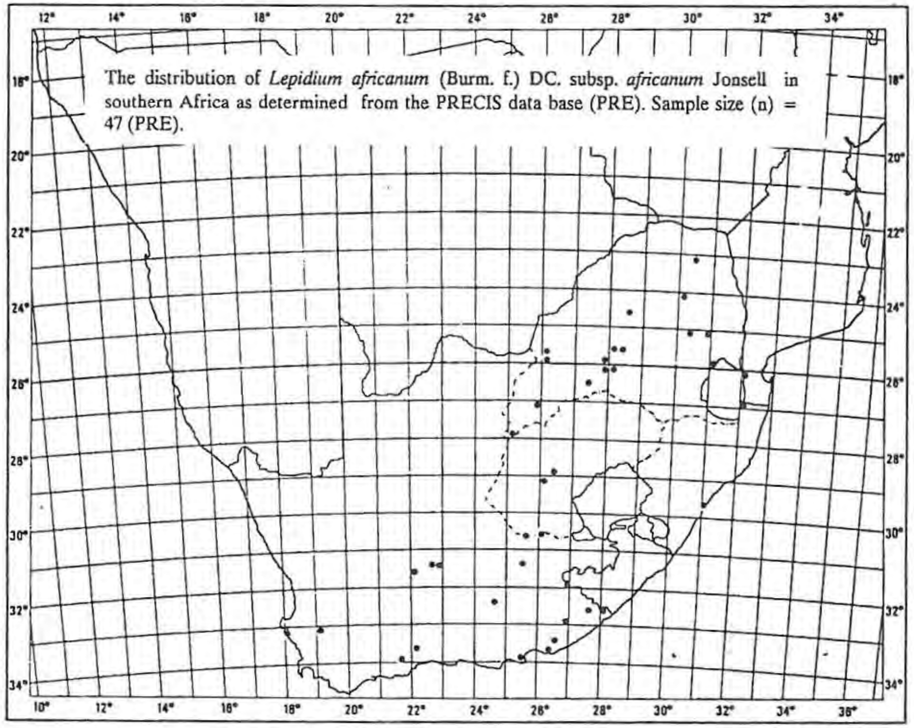
The distribution of *Trichodiadema pygmaeum* L. Bol. in southern Africa as determined from the PRECIS data base (PRE). Sample size (n) = 32 (PRE).



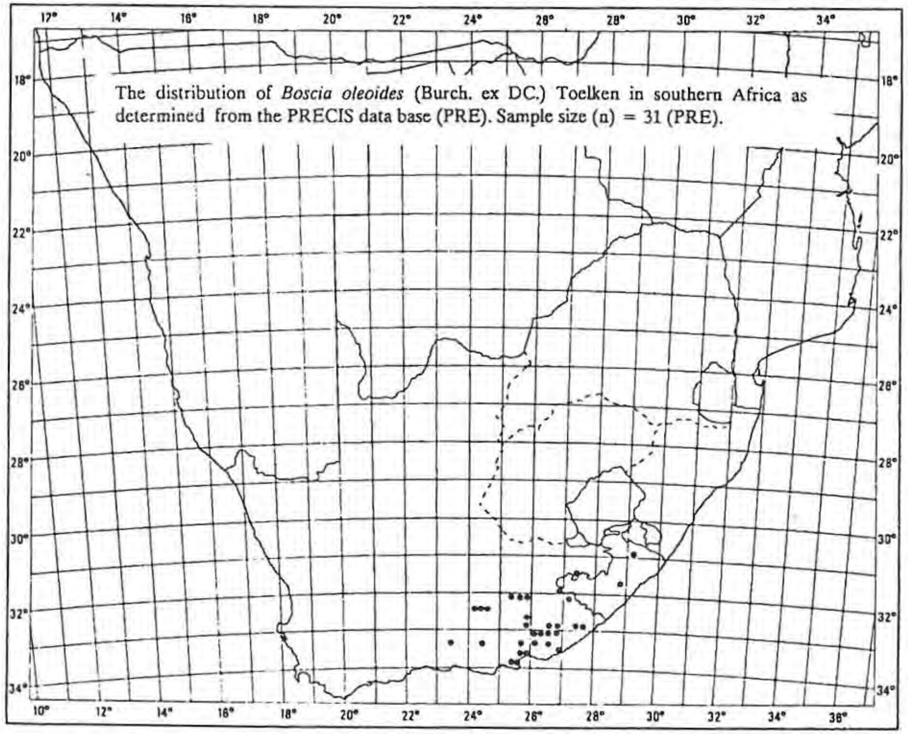
The distribution of *Anacampseros telephiastrum* DC.in southern Africa as determined from the PRECIS data base (PRE). Sample size (n) = 12 (PRE).



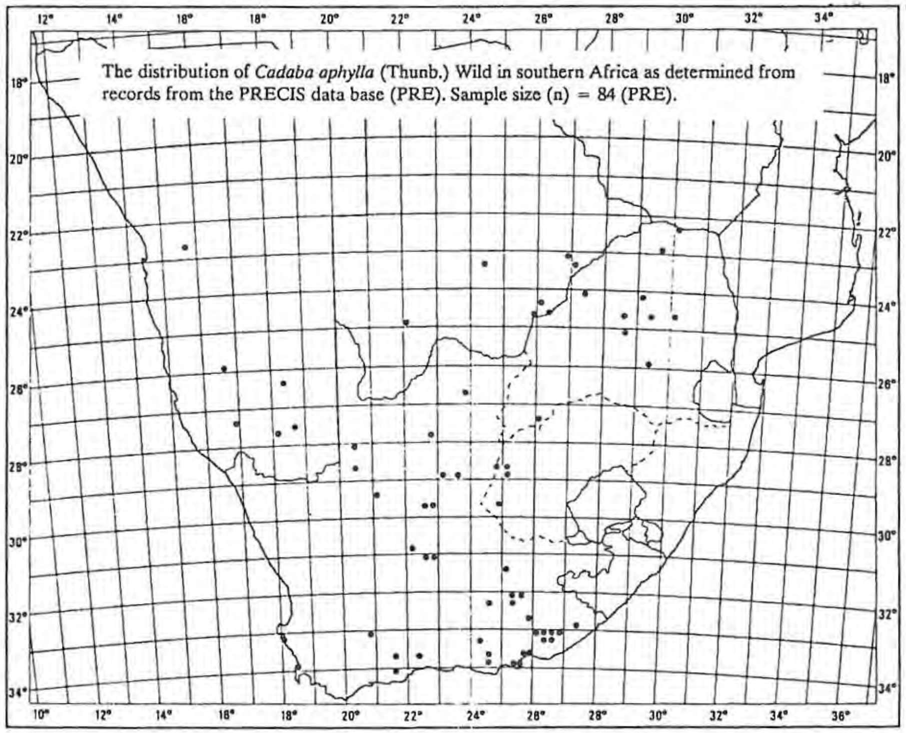
The distribution of *Portulacaria afra* Jacq. in southern Africa as determined from the PRECIS data base (PRE). Sample size (n) = 33 (PRE)



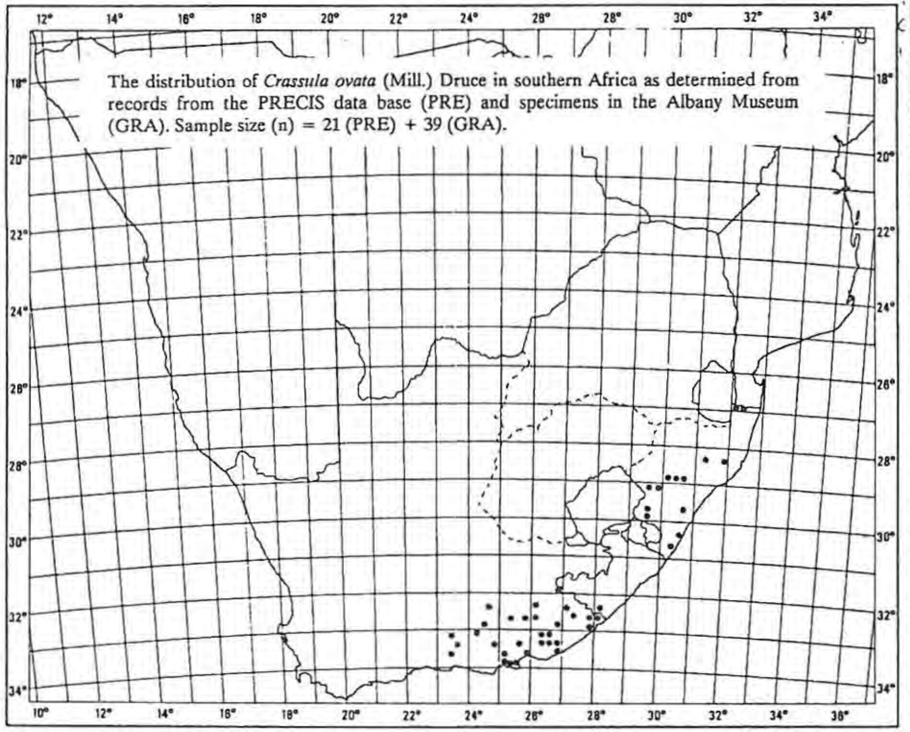
The distribution of *Lepidium africanum* (Burm. f.) DC. subsp. *africanum* Jonsell in southern Africa as determined from the PRECIS data base (PRE). Sample size (n) = 47 (PRE).



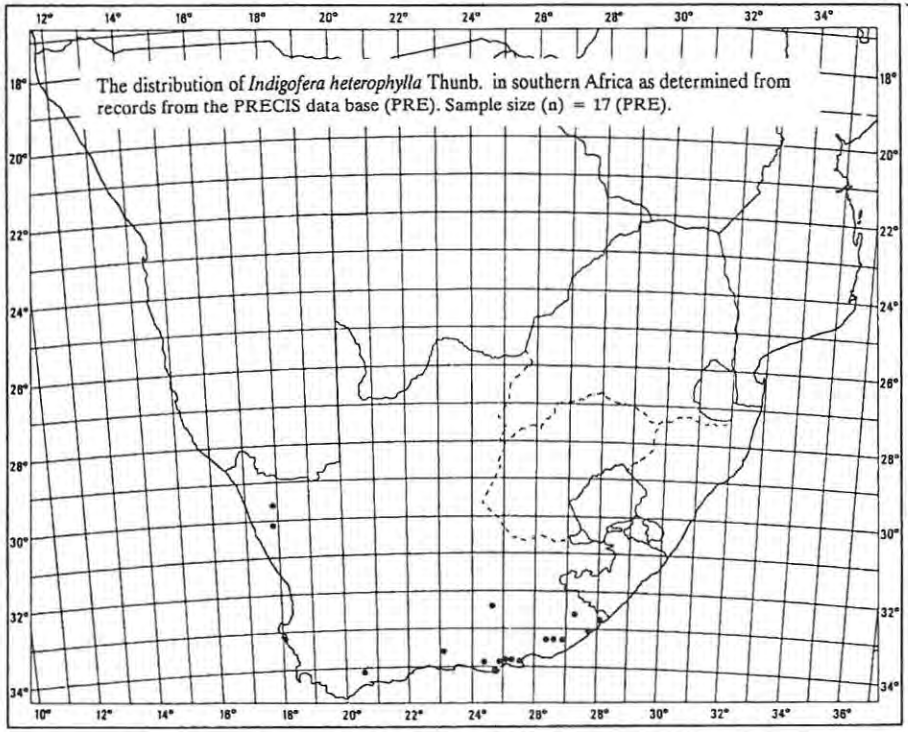
The distribution of *Boscia oleoides* (Burch. ex DC.) Toelken in southern Africa as determined from the PRECIS data base (PRE). Sample size (n) = 31 (PRE).



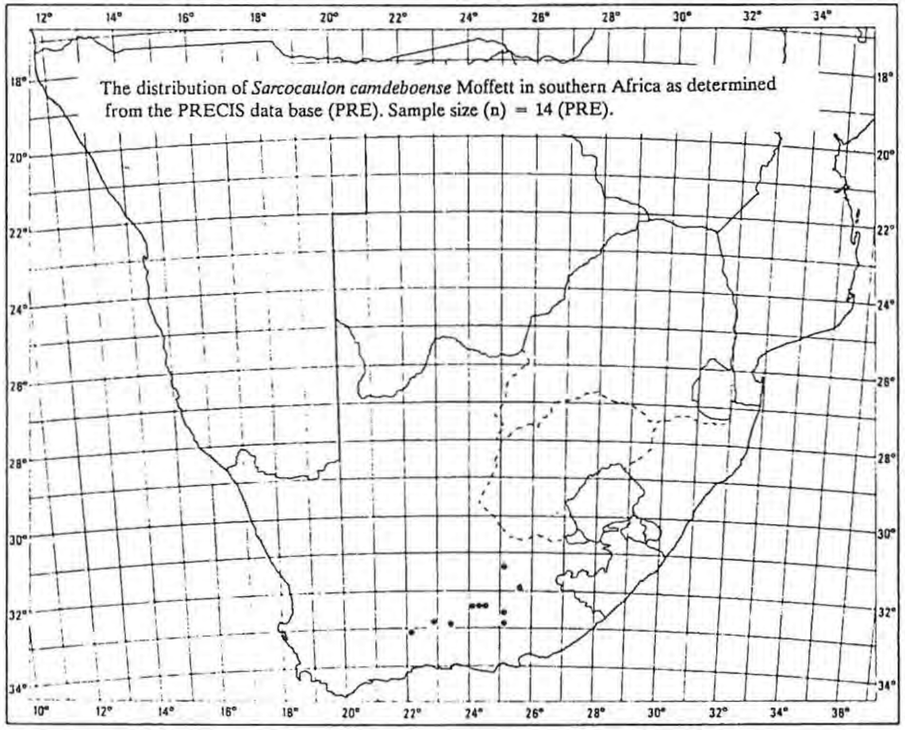
The distribution of *Cadaba aphylla* (Thunb.) Wild in southern Africa as determined from records from the PRECIS data base (PRE). Sample size (n) = 84 (PRE).



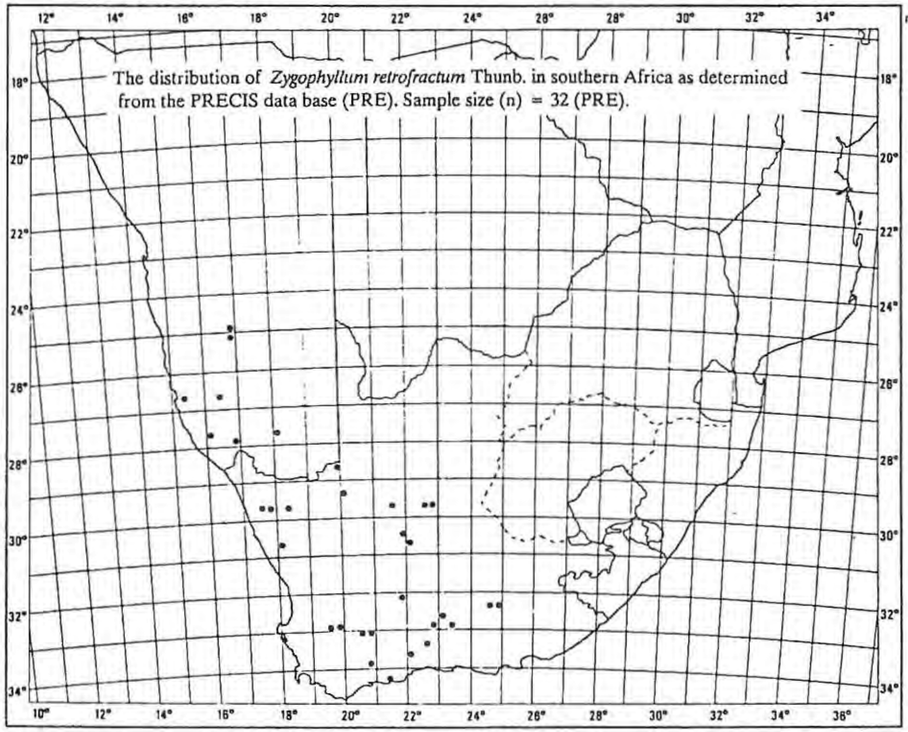
The distribution of *Crassula ovata* (Mill.) Druce in southern Africa as determined from records from the PRECIS data base (PRE) and specimens in the Albany Museum (GRA). Sample size (n) = 21 (PRE) + 39 (GRA).



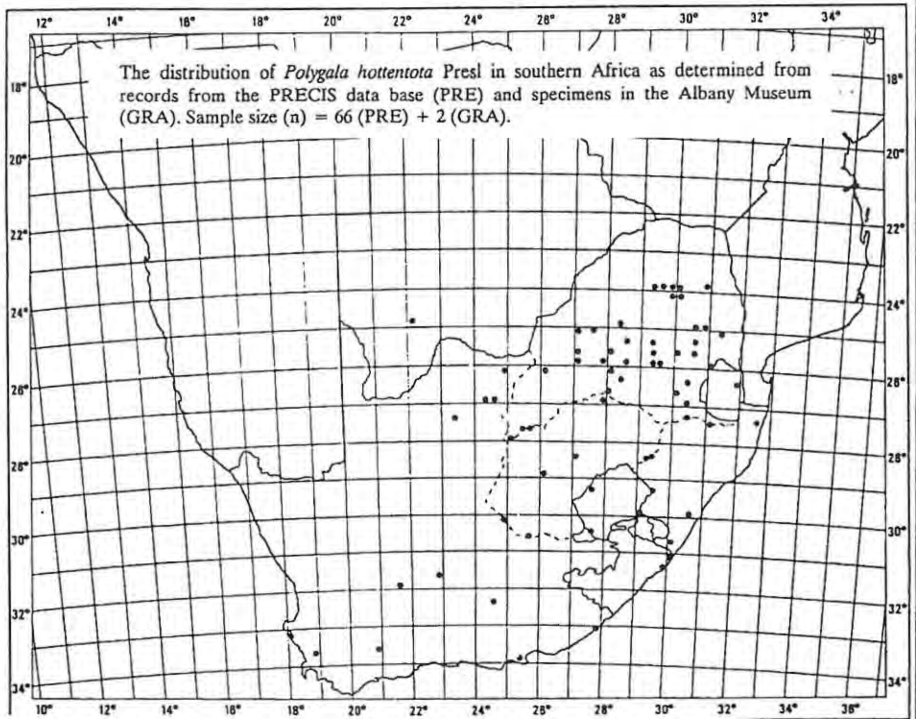
The distribution of *Indigofera heterophylla* Thunb. in southern Africa as determined from records from the PRECIS data base (PRE). Sample size (n) = 17 (PRE).



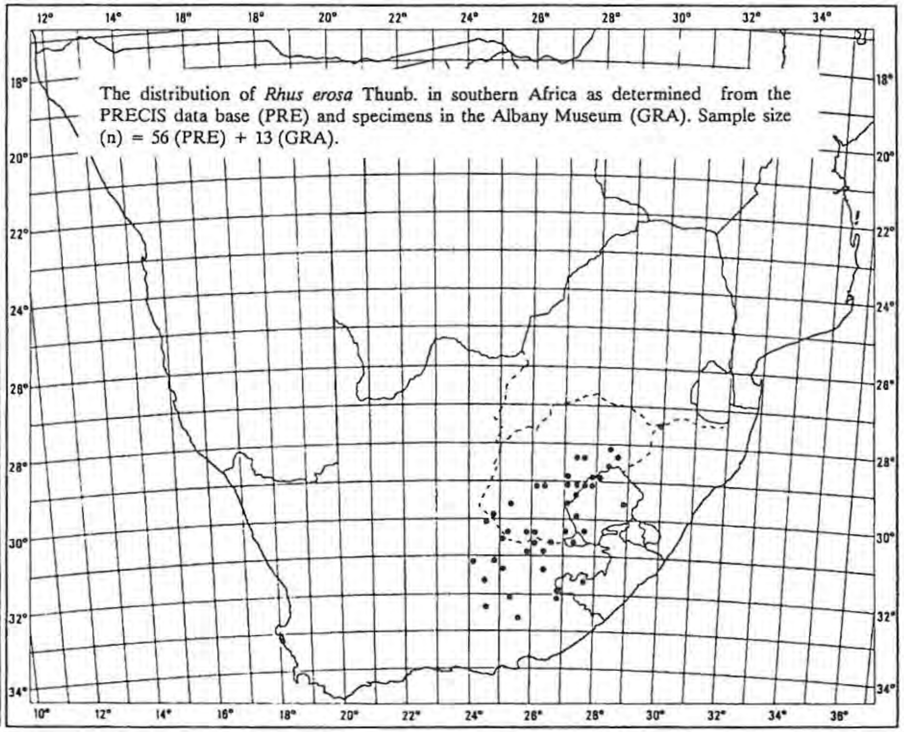
The distribution of *Sarcocaulon camdeboense* Moffett in southern Africa as determined from the PRECIS data base (PRE). Sample size (n) = 14 (PRE).



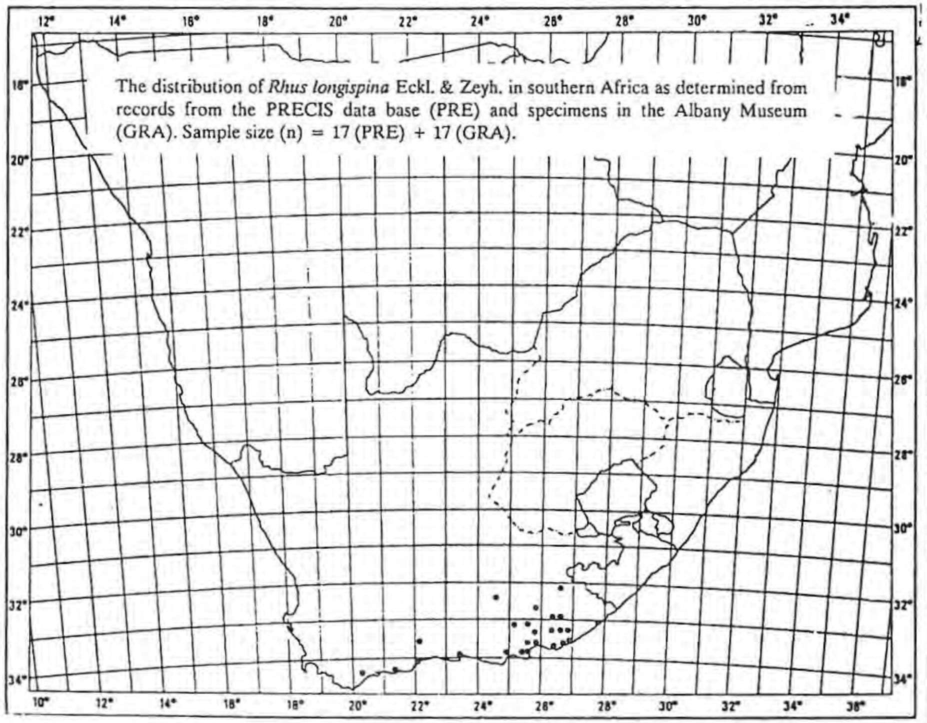
The distribution of *Zygophyllum retrofractum* Thunb. in southern Africa as determined from the PRECIS data base (PRE). Sample size (n) = 32 (PRE).



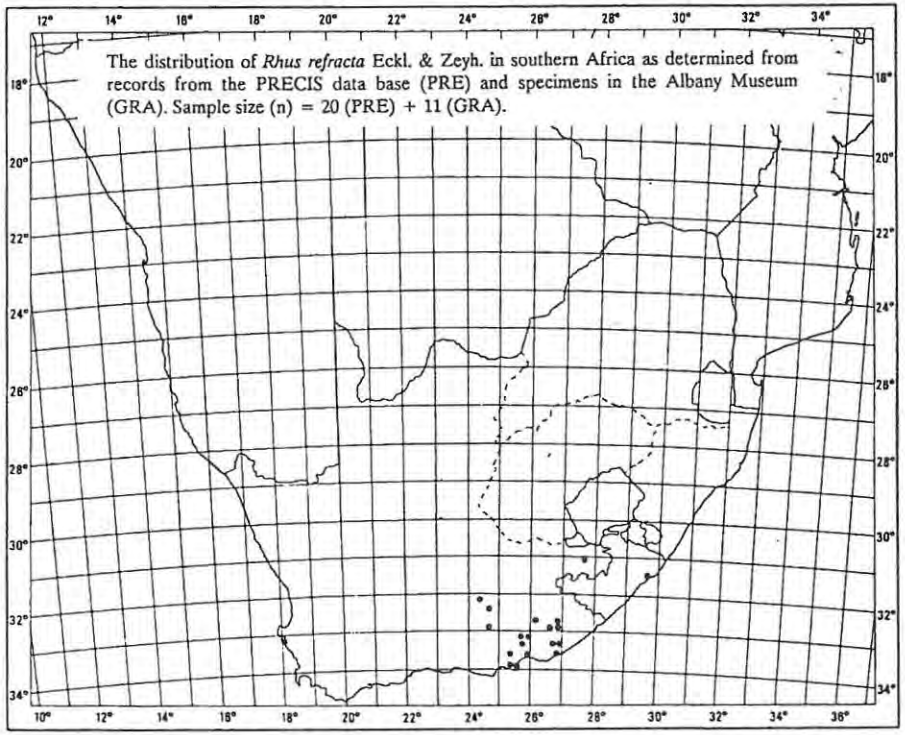
The distribution of *Polygala hottentota* Presl in southern Africa as determined from records from the PRECIS data base (PRE) and specimens in the Albany Museum (GRA). Sample size (n) = 66 (PRE) + 2 (GRA).



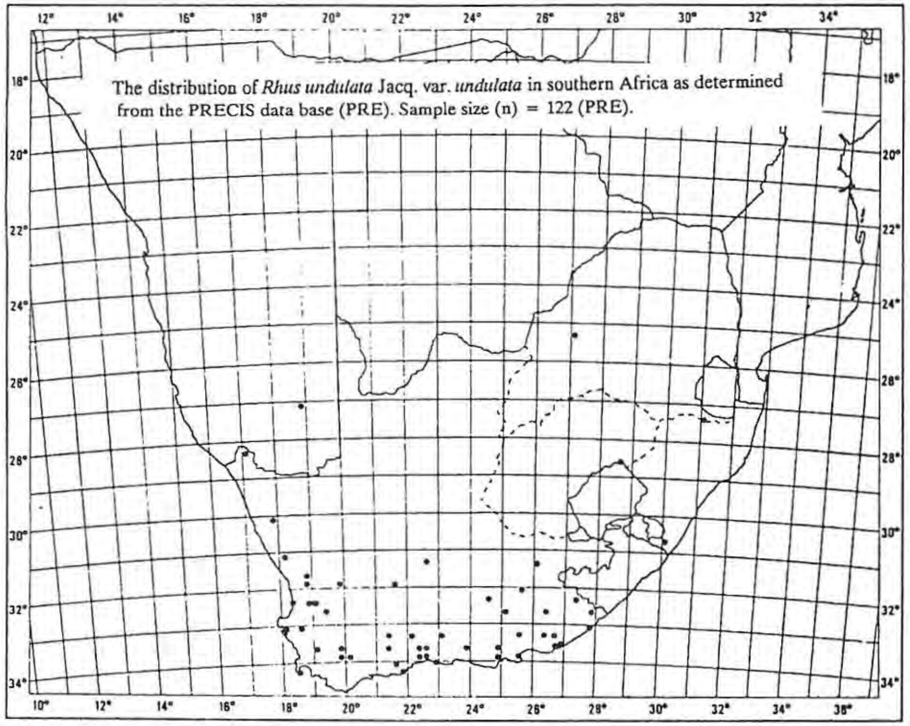
The distribution of *Rhus erosa* Thunb. in southern Africa as determined from the PRECIS data base (PRE) and specimens in the Albany Museum (GRA). Sample size (n) = 56 (PRE) + 13 (GRA).



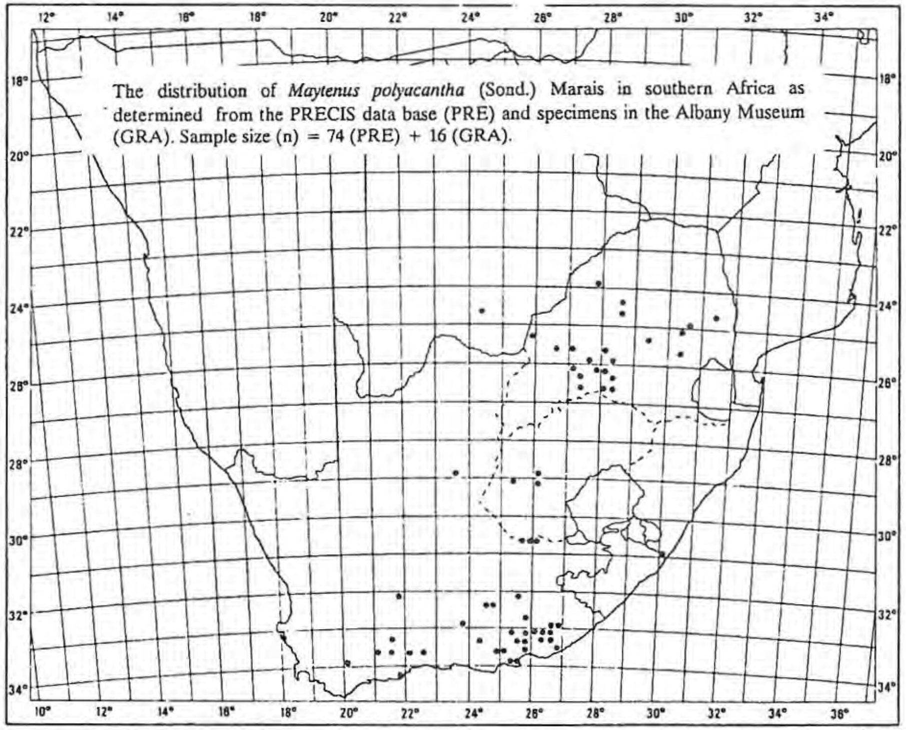
The distribution of *Rhus longispina* Eckl. & Zeyh. in southern Africa as determined from records from the PRECIS data base (PRE) and specimens in the Albany Museum (GRA). Sample size (n) = 17 (PRE) + 17 (GRA).



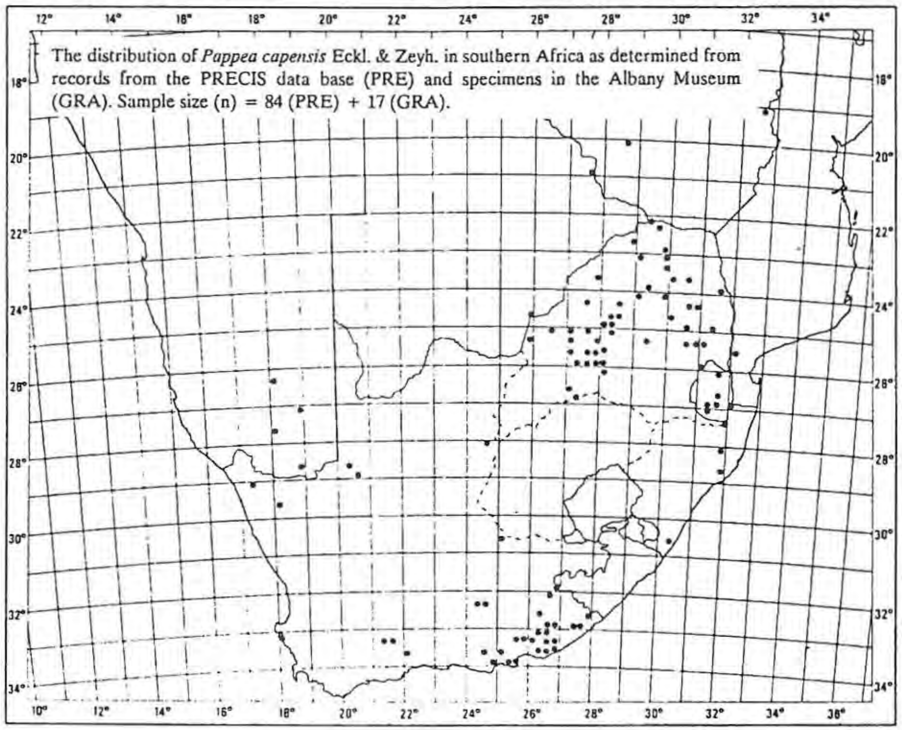
The distribution of *Rhus refracta* Eckl. & Zeyh. in southern Africa as determined from records from the PRECIS data base (PRE) and specimens in the Albany Museum (GRA). Sample size (n) = 20 (PRE) + 11 (GRA).



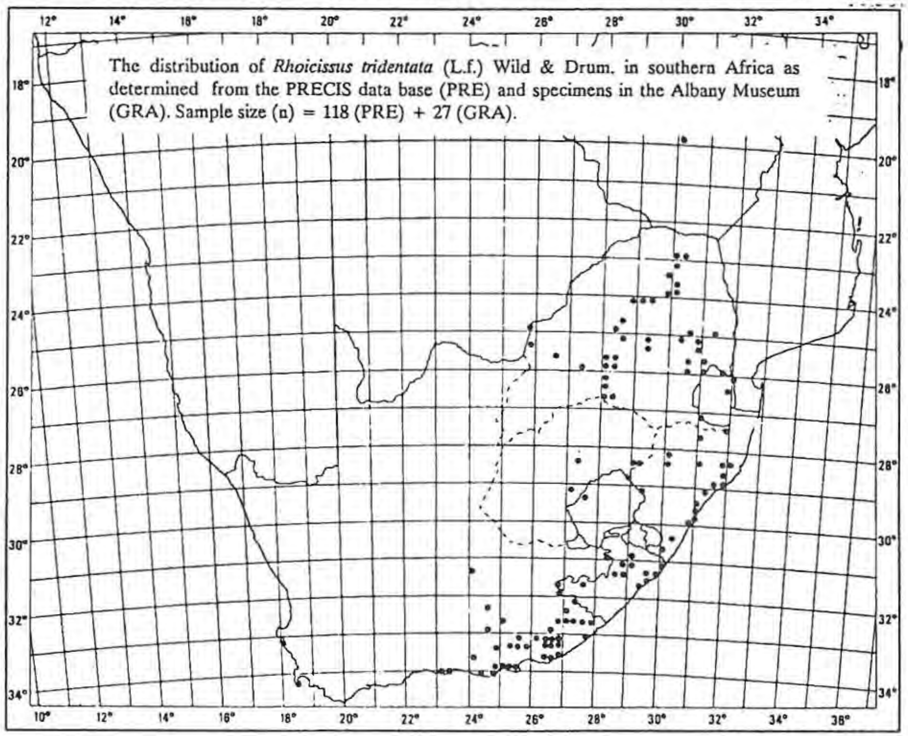
The distribution of *Rhus undulata* Jacq. var. *undulata* in southern Africa as determined from the PRECIS data base (PRE). Sample size (n) = 122 (PRE).



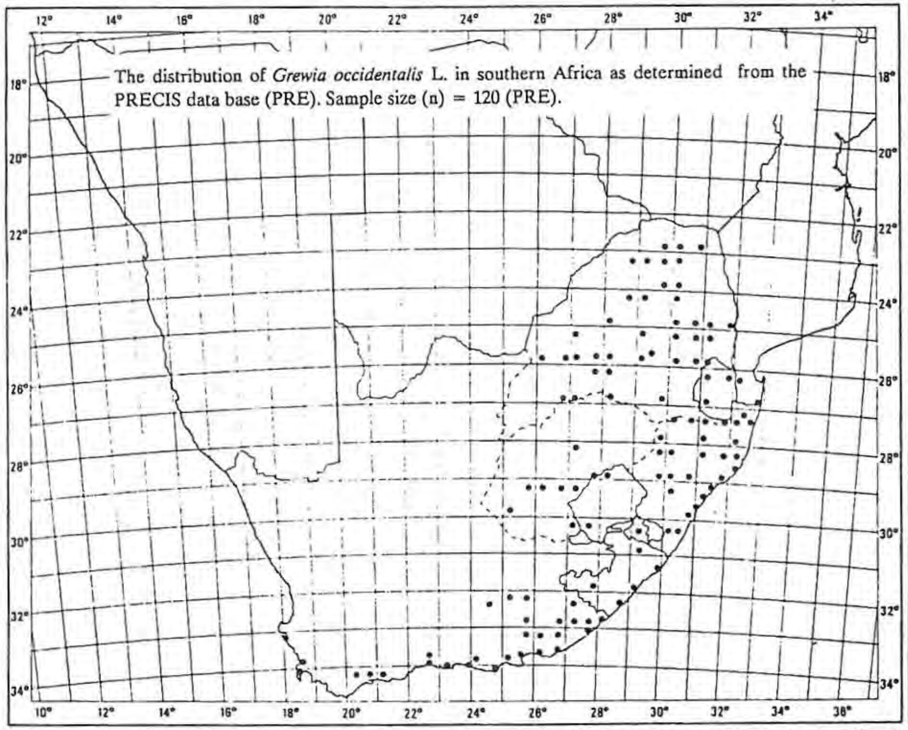
The distribution of *Maytenus polyacantha* (Sond.) Marais in southern Africa as determined from the PRECIS data base (PRE) and specimens in the Albany Museum (GRA). Sample size (n) = 74 (PRE) + 16 (GRA).



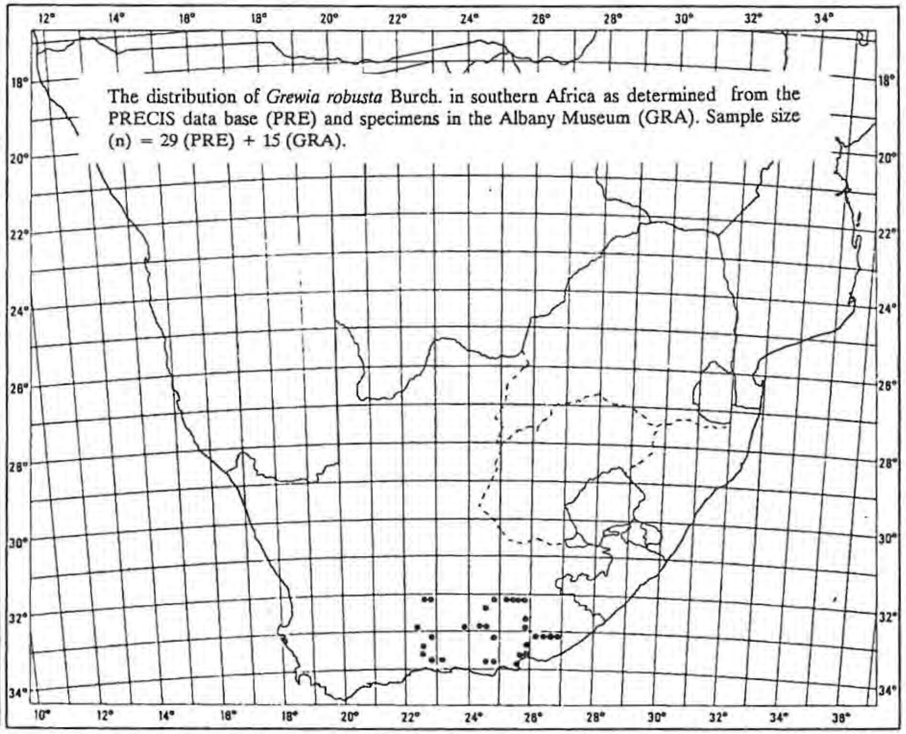
The distribution of *Pappea capensis* Eckl. & Zeyh. in southern Africa as determined from records from the PRECIS data base (PRE) and specimens in the Albany Museum (GRA). Sample size (n) = 84 (PRE) + 17 (GRA).



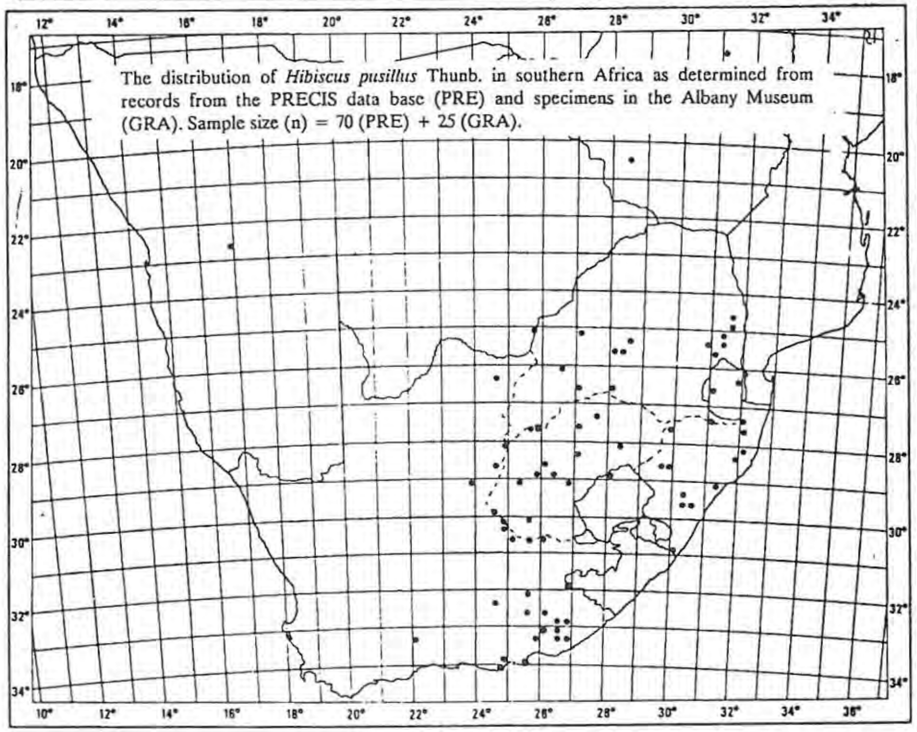
The distribution of *Rhoicissus tridentata* (L.f.) Wild & Drum. in southern Africa as determined from the PRECIS data base (PRE) and specimens in the Albany Museum (GRA). Sample size (n) = 118 (PRE) + 27 (GRA).



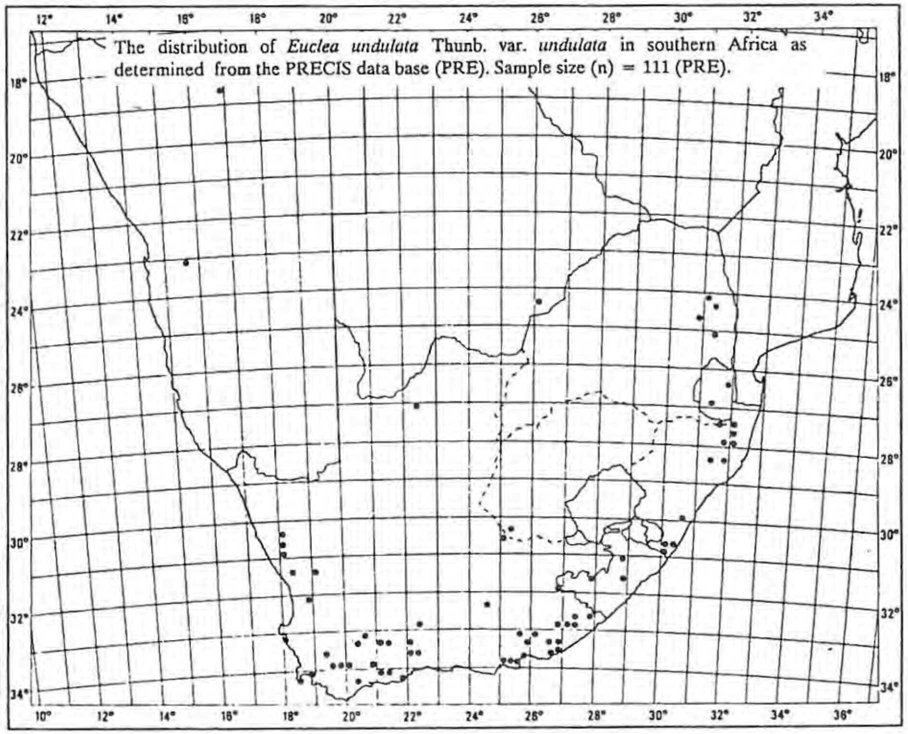
The distribution of *Grewia occidentalis* L. in southern Africa as determined from the PRECIS data base (PRE). Sample size (n) = 120 (PRE).



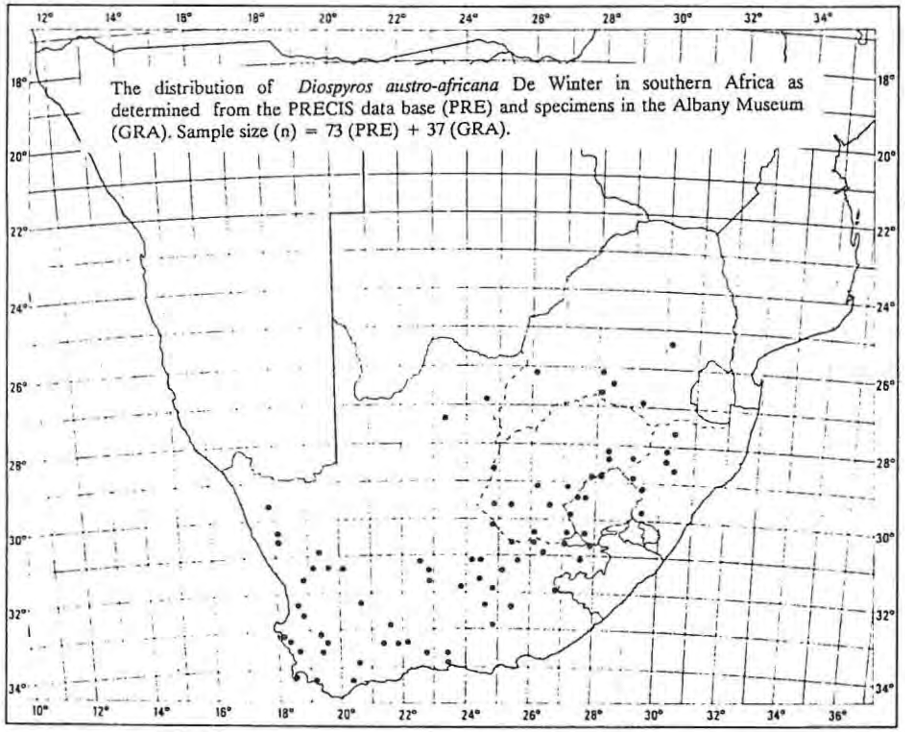
The distribution of *Grewia robusta* Burch. in southern Africa as determined from the PRECIS data base (PRE) and specimens in the Albany Museum (GRA). Sample size (n) = 29 (PRE) + 15 (GRA).



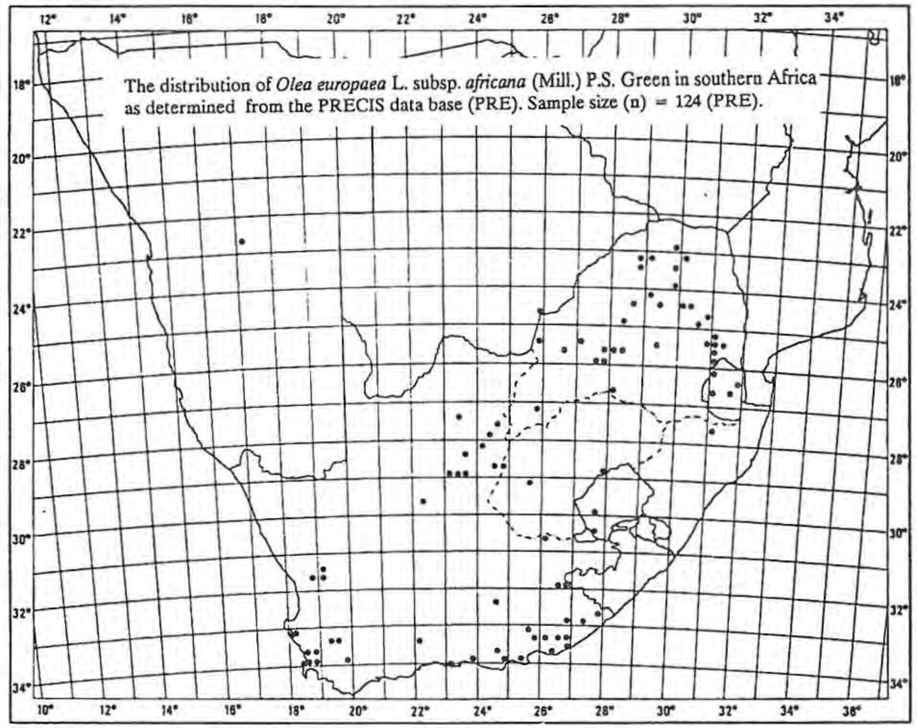
The distribution of *Hibiscus pusillus* Thunb. in southern Africa as determined from records from the PRECIS data base (PRE) and specimens in the Albany Museum (GRA). Sample size (n) = 70 (PRE) + 25 (GRA).



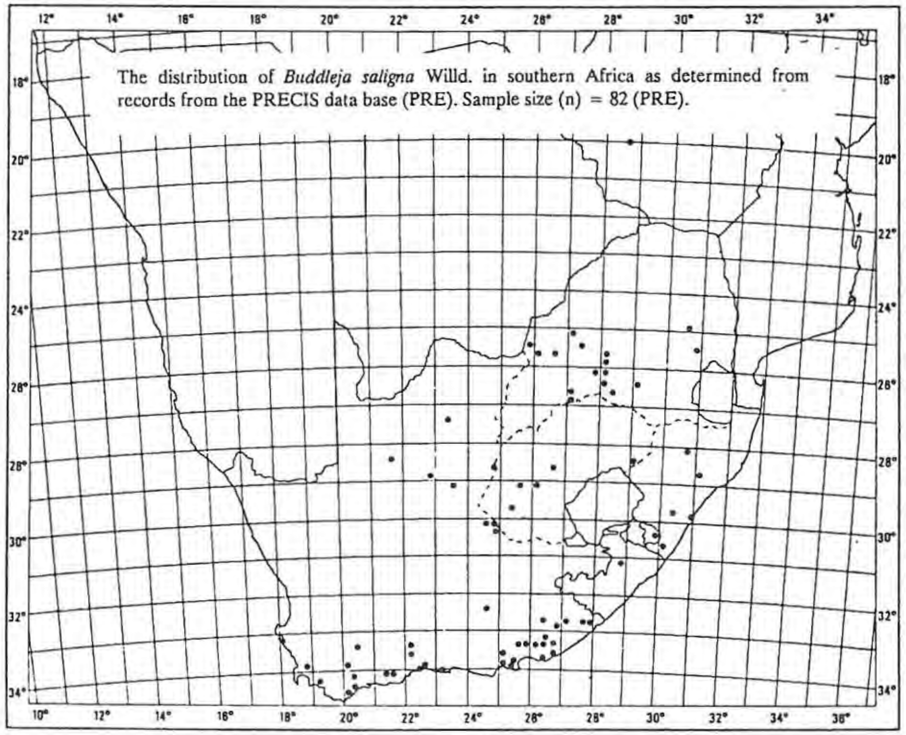
The distribution of *Euclea undulata* Thunb. var. *undulata* in southern Africa as determined from the PRECIS data base (PRE). Sample size (n) = 111 (PRE).



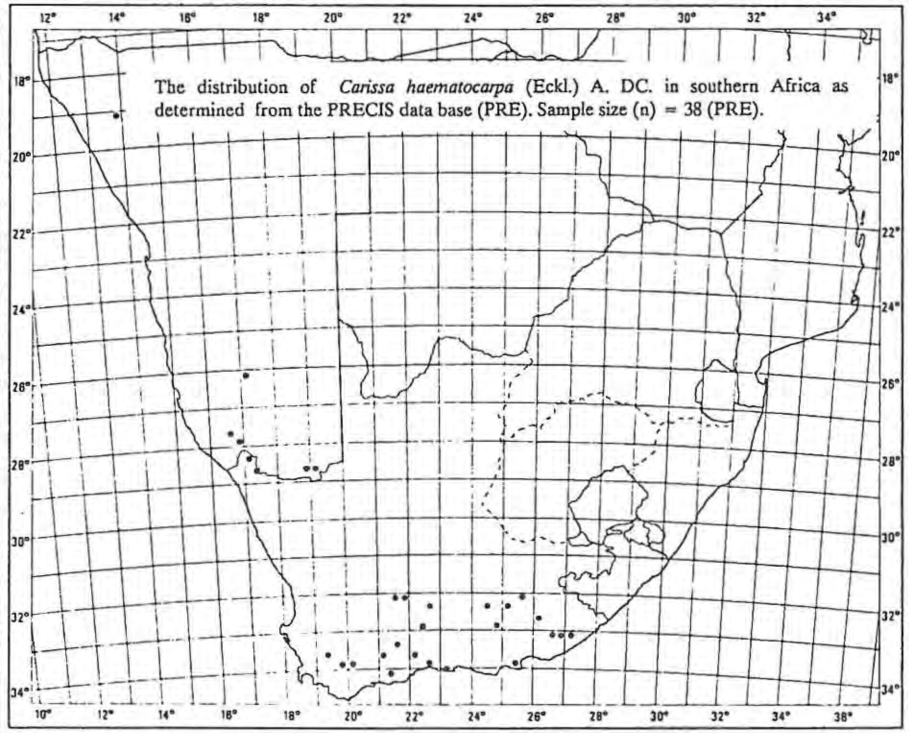
The distribution of *Diospyros austro-africana* De Winter in southern Africa as determined from the PRECIS data base (PRE) and specimens in the Albany Museum (GRA). Sample size (n) = 73 (PRE) + 37 (GRA).



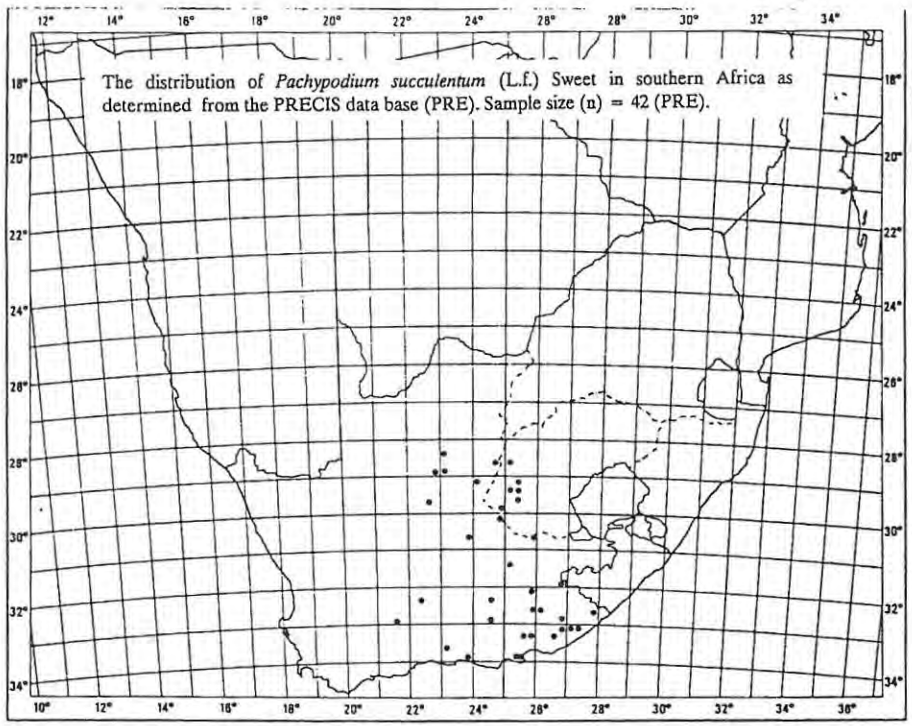
The distribution of *Olea europaea* L. subsp. *africana* (Mill.) P.S. Green in southern Africa as determined from the PRECIS data base (PRE). Sample size (n) = 124 (PRE).



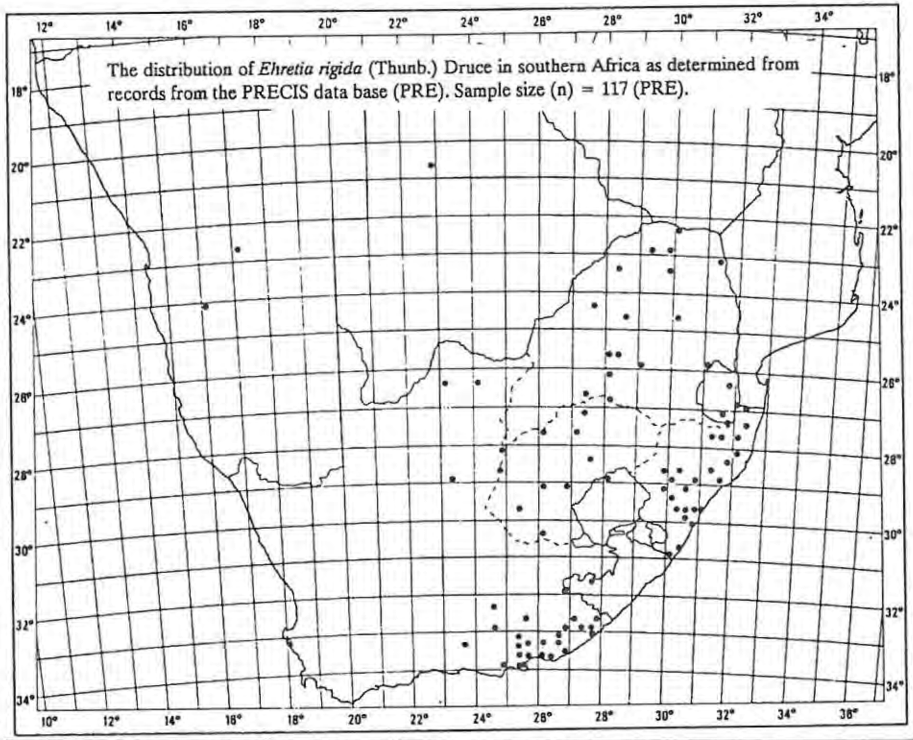
The distribution of *Buddleja saligna* Willd. in southern Africa as determined from records from the PRECIS data base (PRE). Sample size (n) = 82 (PRE).



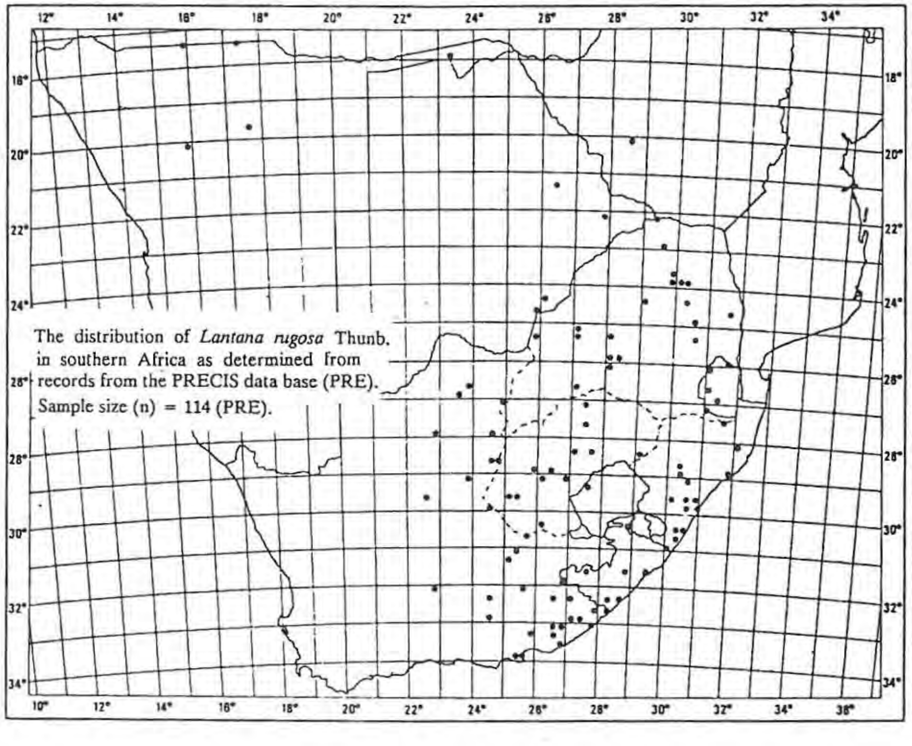
The distribution of *Carissa haematocarpa* (Eckl.) A. DC. in southern Africa as determined from the PRECIS data base (PRE). Sample size (n) = 38 (PRE).



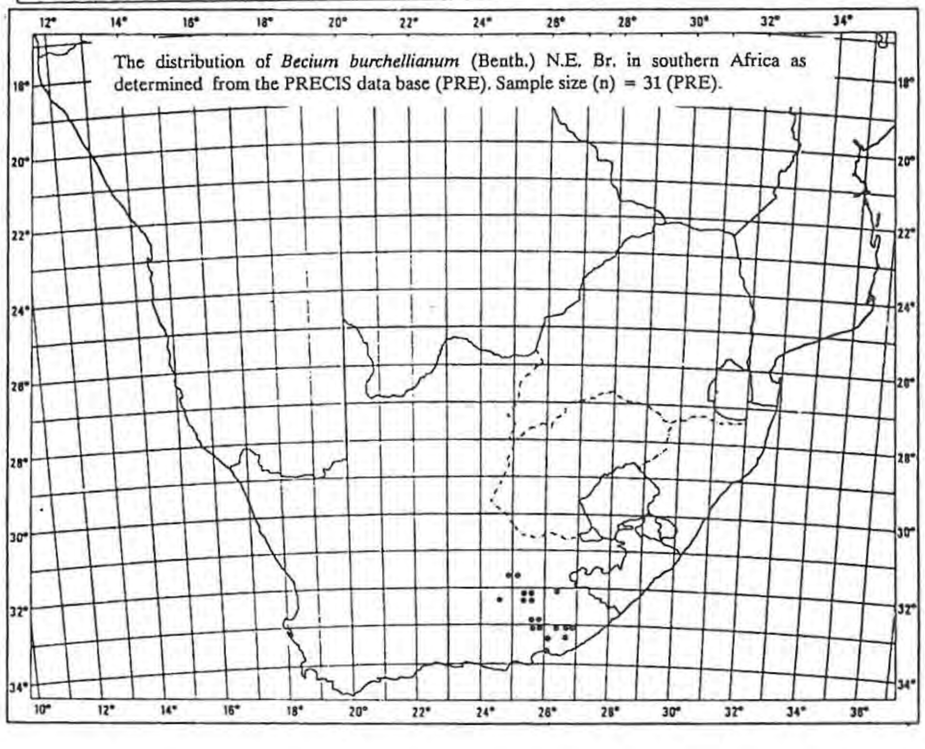
The distribution of *Pachypodium succulentum* (L.f.) Sweet in southern Africa as determined from the PRECIS data base (PRE). Sample size (n) = 42 (PRE).



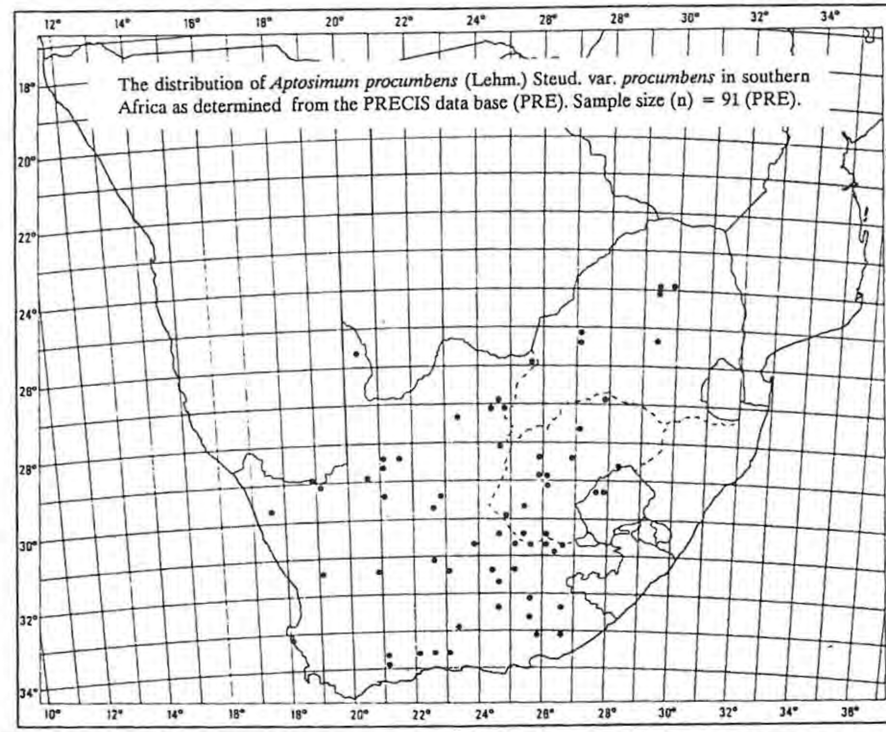
The distribution of *Ehretia rigida* (Thunb.) Druce in southern Africa as determined from records from the PRECIS data base (PRE). Sample size (n) = 117 (PRE).



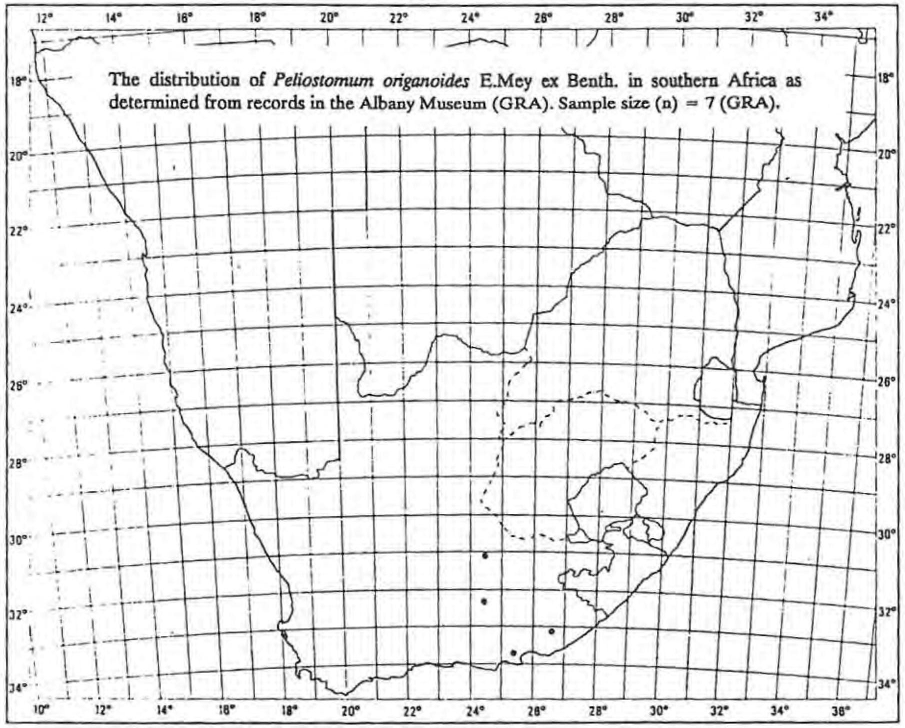
The distribution of *Lantana rugosa* Thunb. in southern Africa as determined from records from the PRECIS data base (PRE). Sample size (n) = 114 (PRE).



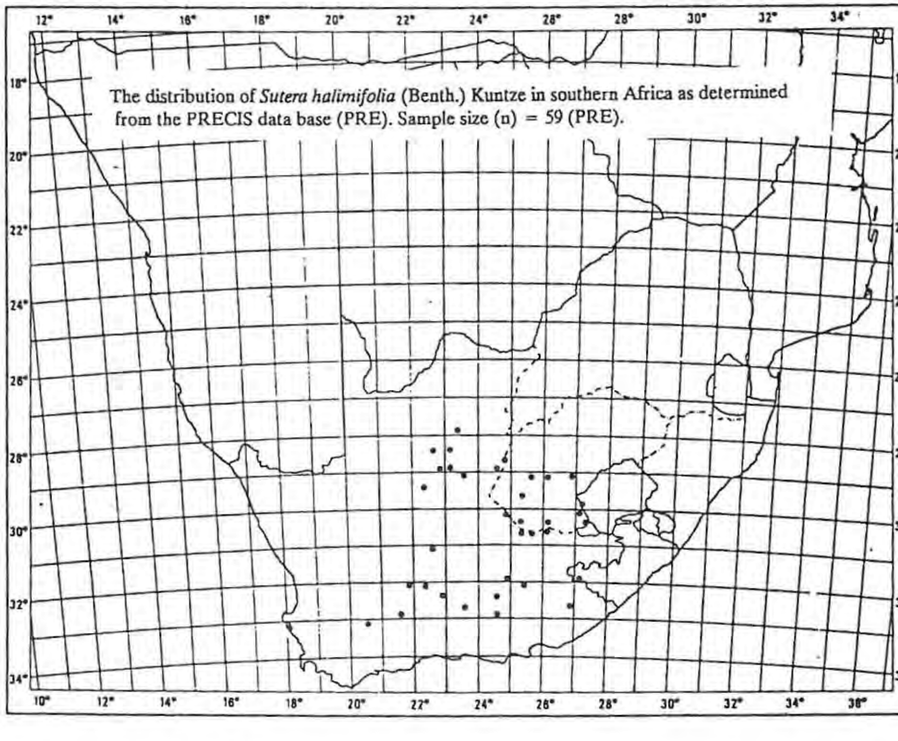
The distribution of *Becium burchellianum* (Benth.) N.E. Br. in southern Africa as determined from the PRECIS data base (PRE). Sample size (n) = 31 (PRE).



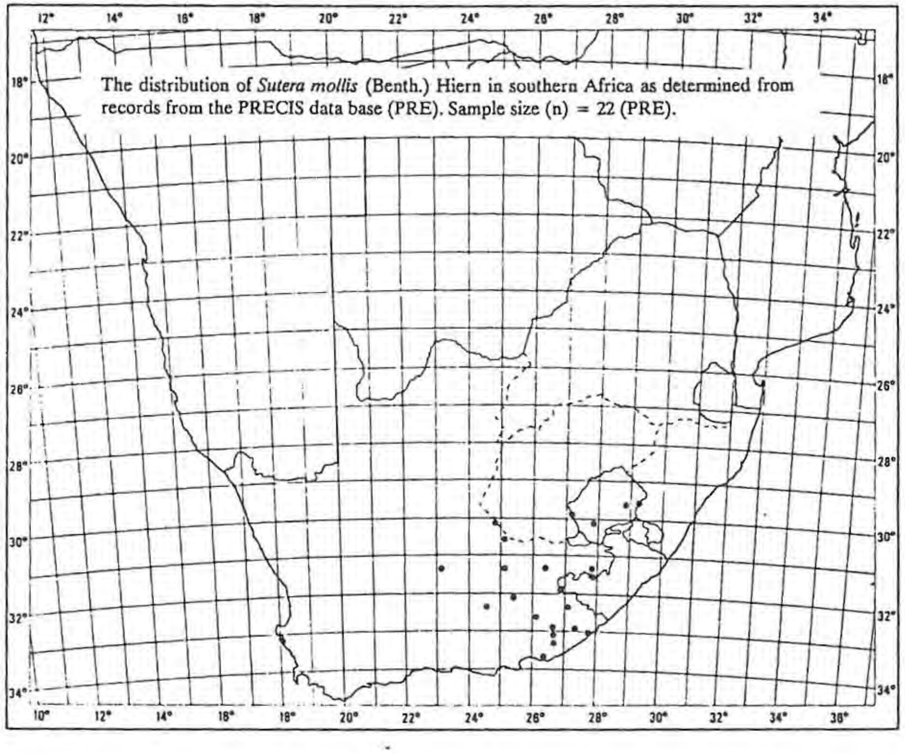
The distribution of *Aptosimum procumbens* (Lehm.) Steud. var. *procumbens* in southern Africa as determined from the PRECIS data base (PRE). Sample size (n) = 91 (PRE).



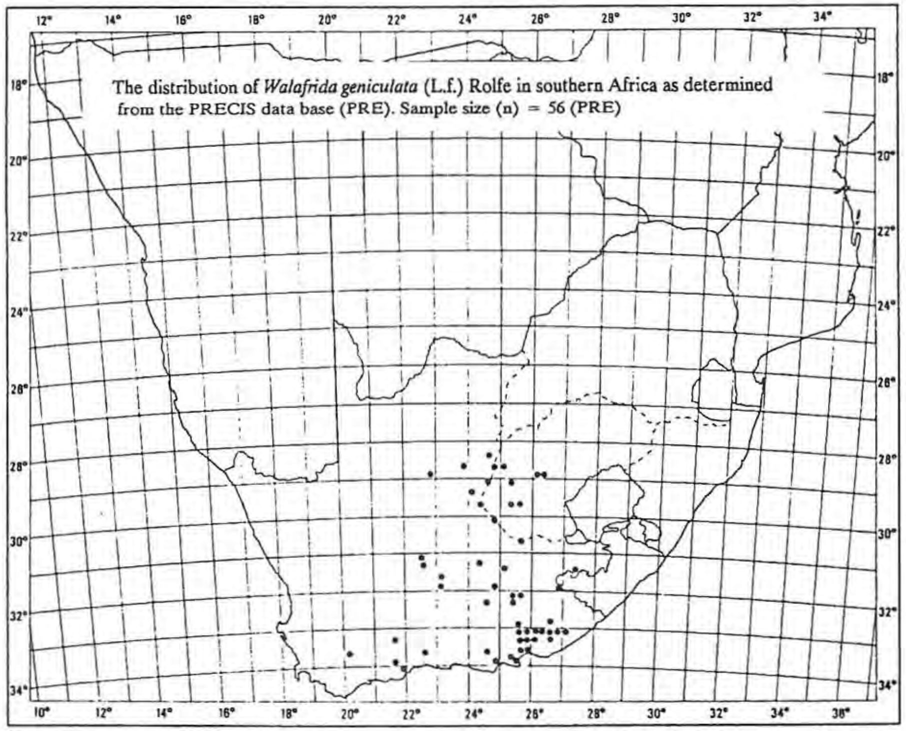
The distribution of *Peliostomum origanoides* E.Mey ex Benth. in southern Africa as determined from records in the Albany Museum (GRA). Sample size (n) = 7 (GRA).



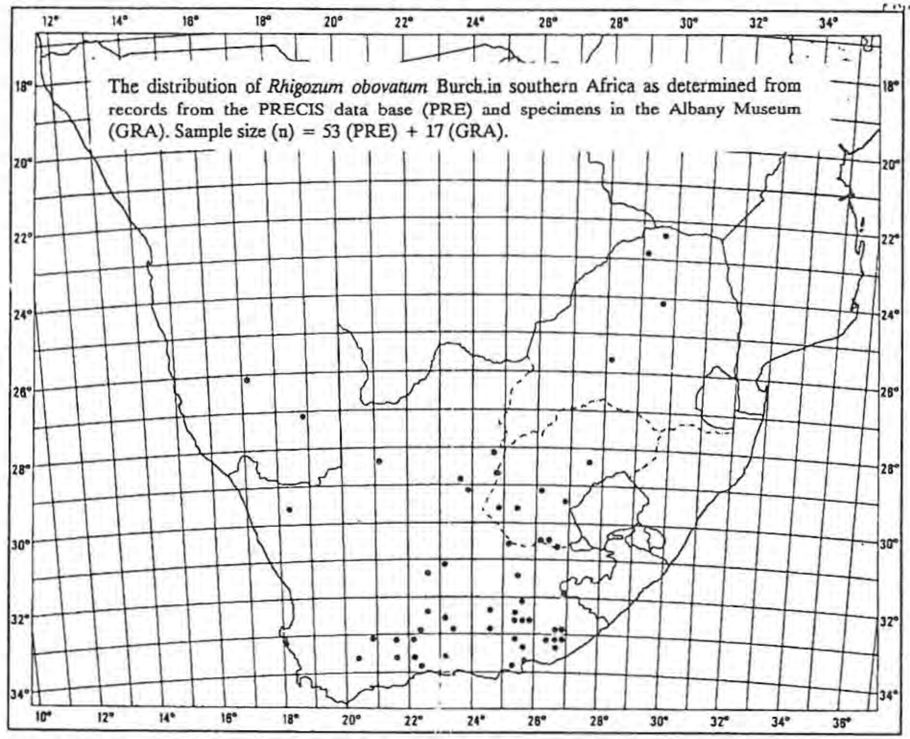
The distribution of *Sutera halimifolia* (Benth.) Kuntze in southern Africa as determined from the PRECIS data base (PRE). Sample size (n) = 59 (PRE).



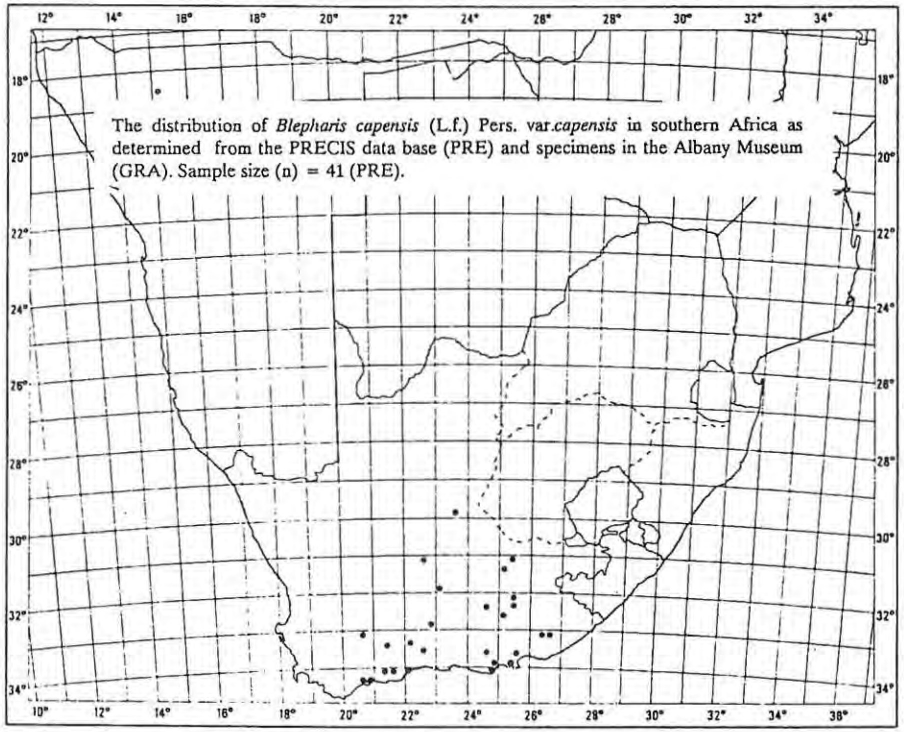
The distribution of *Sutera mollis* (Benth.) Hiern in southern Africa as determined from records from the PRECIS data base (PRE). Sample size (n) = 22 (PRE).



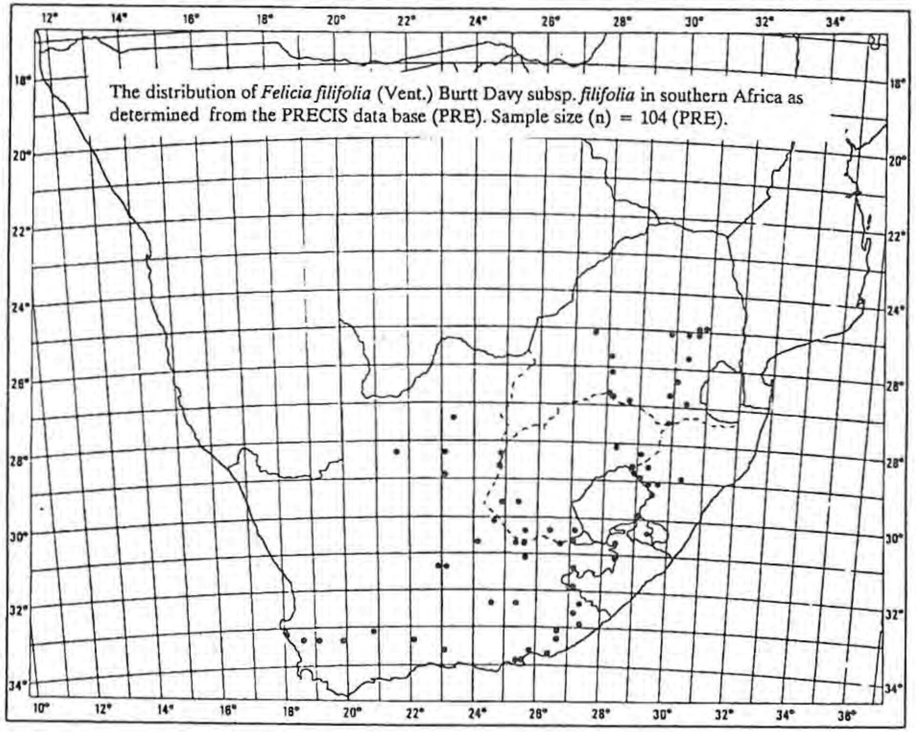
The distribution of *Walafrida geniculata* (L.f.) Rolfe in southern Africa as determined from the PRECIS data base (PRE). Sample size (n) = 56 (PRE)



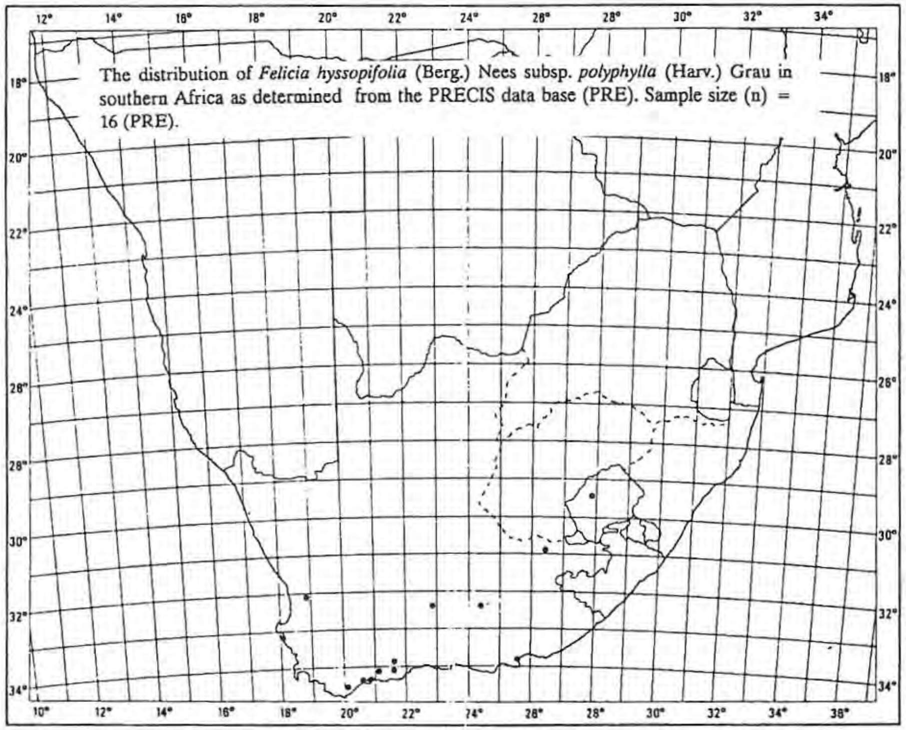
The distribution of *Rhigozum obovatum* Burch.in southern Africa as determined from records from the PRECIS data base (PRE) and specimens in the Albany Museum (GRA). Sample size (n) = 53 (PRE) + 17 (GRA).



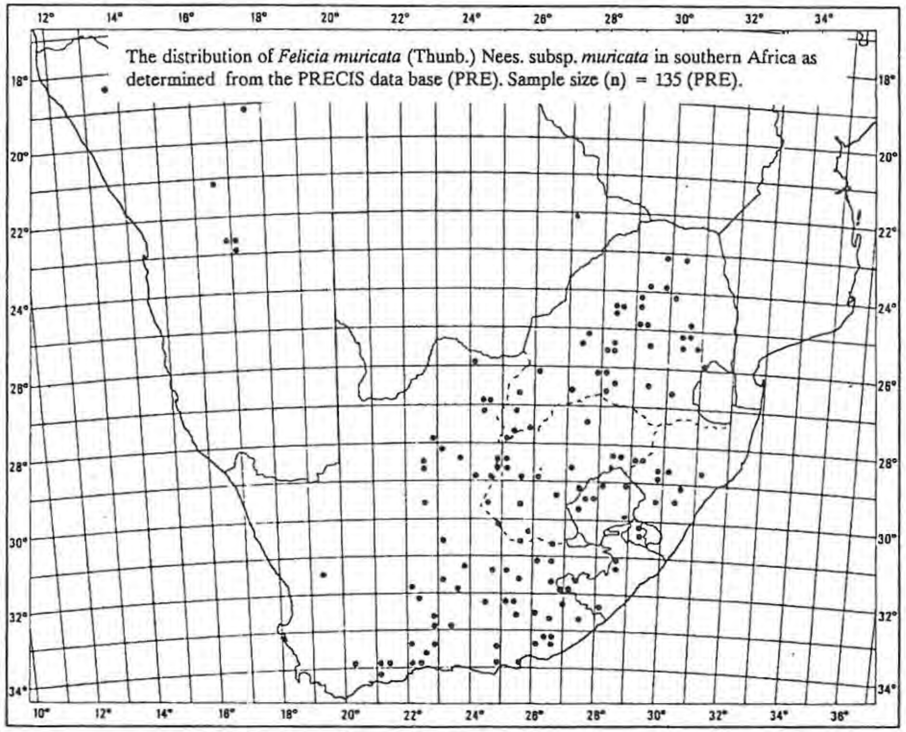
The distribution of *Blepharis capensis* (L.f.) Pers. var.*capensis* in southern Africa as determined from the PRECIS data base (PRE) and specimens in the Albany Museum (GRA). Sample size (n) = 41 (PRE).



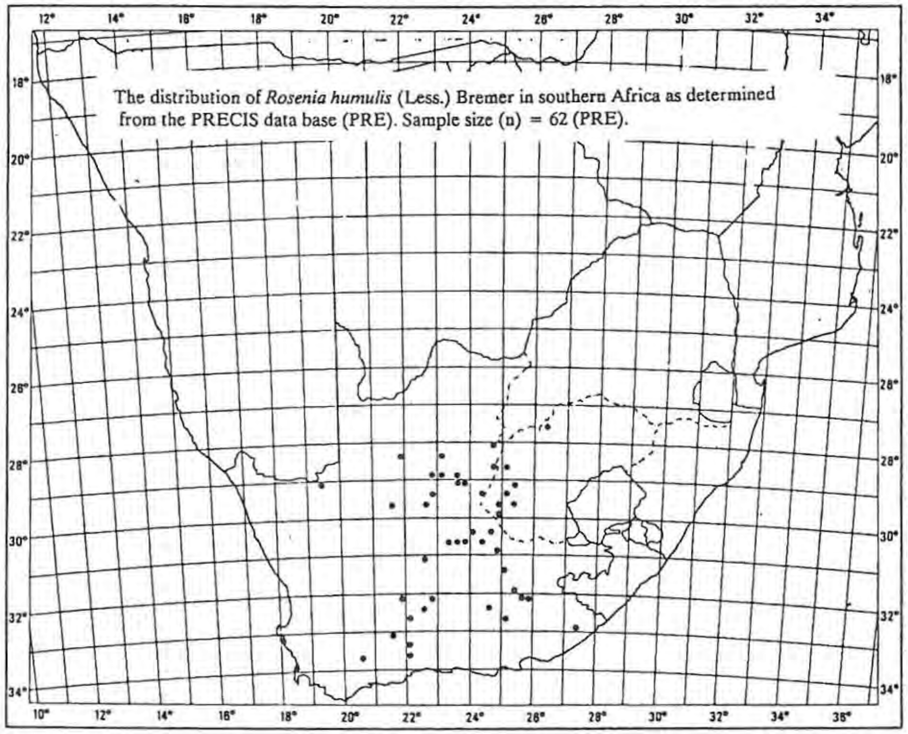
The distribution of *Felicia filifolia* (Vent.) Burtt Davy subsp. *filifolia* in southern Africa as determined from the PRECIS data base (PRE). Sample size (n) = 104 (PRE).



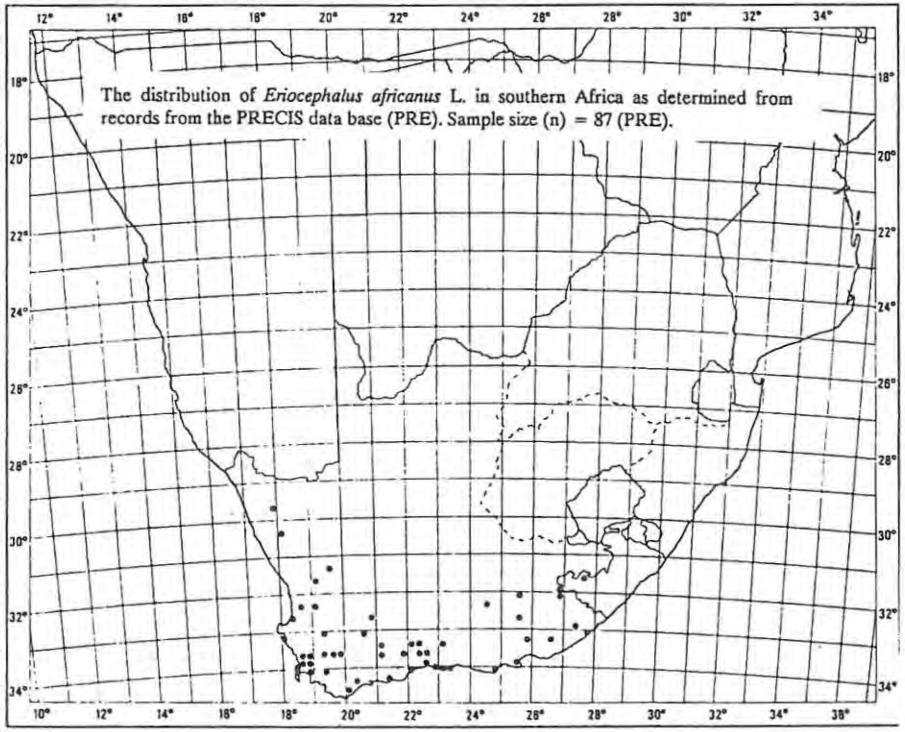
The distribution of *Felicia hyssopifolia* (Berg.) Nees subsp. *polyphylla* (Harv.) Grau in southern Africa as determined from the PRECIS data base (PRE). Sample size (n) = 16 (PRE).



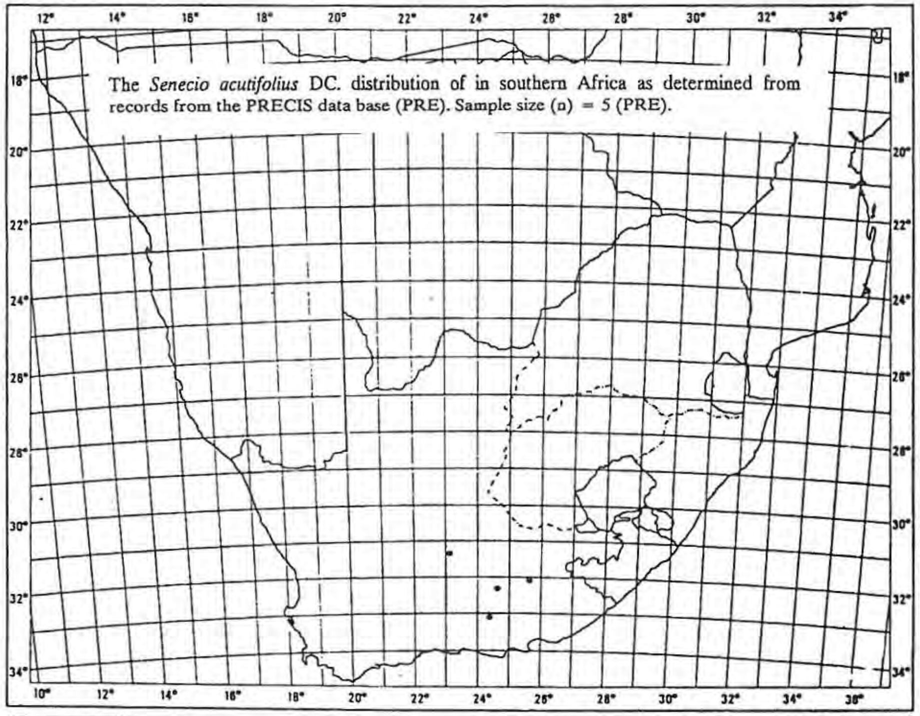
The distribution of *Felicia muricata* (Thunb.) Nees. subsp. *muricata* in southern Africa as determined from the PRECIS data base (PRE). Sample size (n) = 135 (PRE).



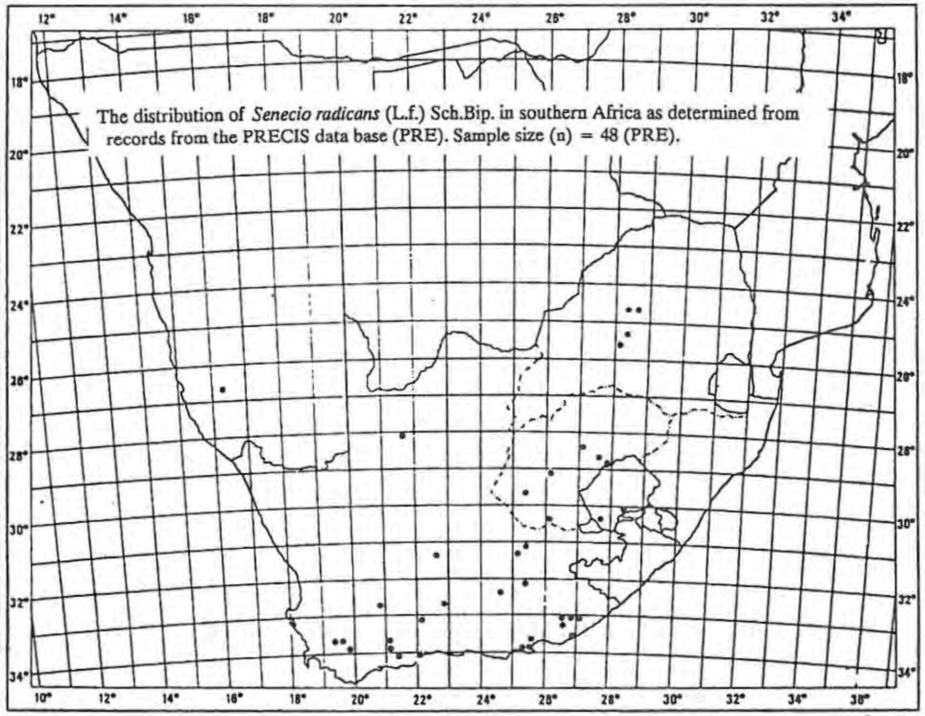
The distribution of *Rosenia humulis* (Less.) Bremer in southern Africa as determined from the PRECIS data base (PRE). Sample size (n) = 62 (PRE).



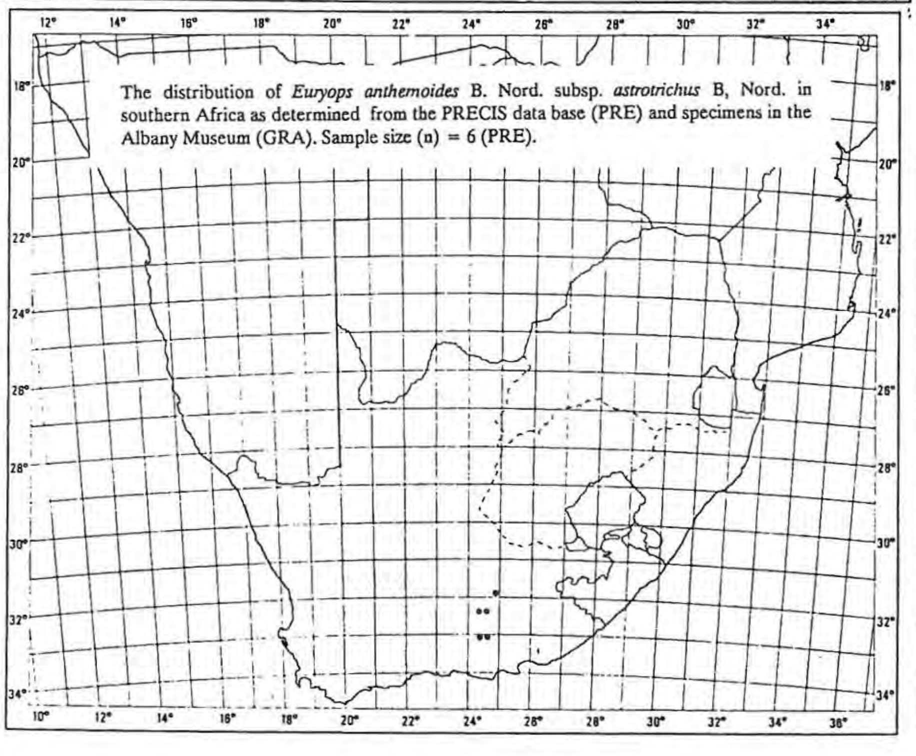
The distribution of *Eriocephalus africanus* L. in southern Africa as determined from records from the PRECIS data base (PRE). Sample size (n) = 87 (PRE).



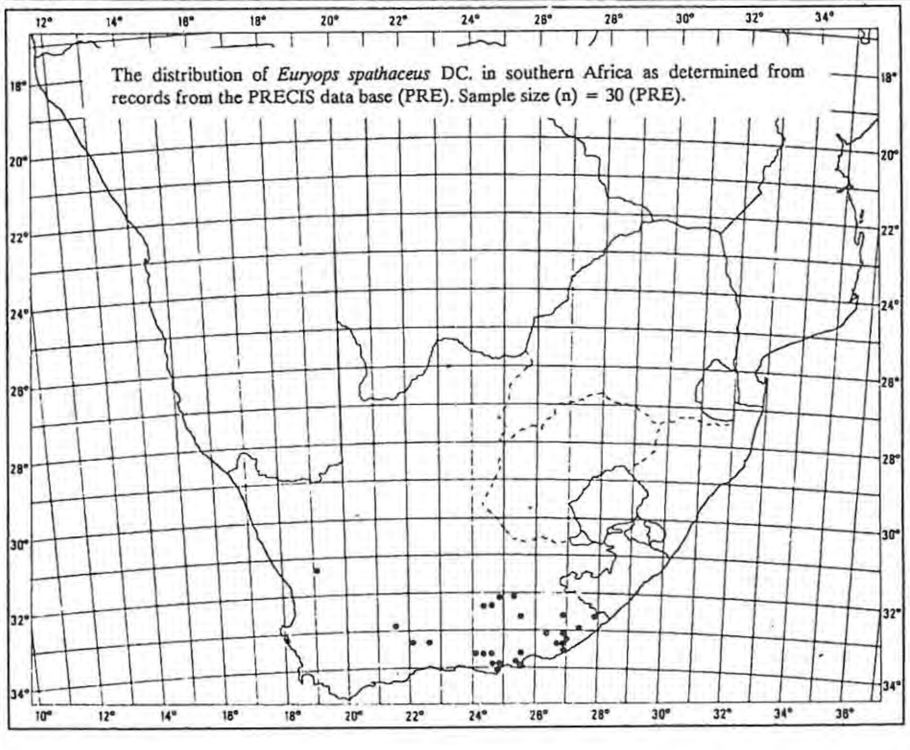
The *Senecio acutifolius* DC. distribution of in southern Africa as determined from records from the PRECIS data base (PRE). Sample size (n) = 5 (PRE).



The distribution of *Senecio radicans* (L.f.) Sch.Bip. in southern Africa as determined from records from the PRECIS data base (PRE). Sample size (n) = 48 (PRE).



The distribution of *Euryops anthemoides* B. Nord. subsp. *astrotrichus* B, Nord. in southern Africa as determined from the PRECIS data base (PRE) and specimens in the Albany Museum (GRA). Sample size (n) = 6 (PRE).



The distribution of *Euryops spathaceus* DC. in southern Africa as determined from records from the PRECIS data base (PRE). Sample size (n) = 30 (PRE).

amdebo and Sneeuberg regions.

	IIIA1	IIIA2	IIIB1	IIIC1	IIID1	IVA1	IVA2	IVA3	VA
1111111 1334556 5093190	111111111111111 022333333444555 378145678012345	111111111112 9334444455691 2234567878522	111111111112222222222222222222222211 8900015667888800002223333444455566678800 9301912140345657891590567025867816790167	1111122222211 15666011112277 26238614566812	11112221111 77775567768 56783633497	22211122 8156016568 1329496542	1121222222 8890150552667 7802815047027	11112 78886 90125	1122 81227 60046
1111111 3000000 3811111 0000000	11111111111111 900000000000000 792840021111414 000000000000500	111111111111 1000000000302 4281111111100 2000000000800	1 11 11111 11 1111 11 7077773078877712334773477443377767702477 3566990160099951108350750060534439501266 0000000000000000000000000200000200002000	1 11111 80777224337777 05966009779999 00000000000000	 77776777777 99999309999 00000000000	 9859999968 0041817232 9000000000	1 1 1 7899050467670 9801650069700 0000100000000	 77774 99999 00000	 76878 70022 06000
6333333 0777777	233333333333333 577777777777777	3333333333333 7777777777777	3333336333333333336333633333333333333333 6766660788888886680888088886888888867766	33333436333333 87888270778888	33333333333 88888888868	2322332222 5755775545	2222223233223 5555537477557	22222 55554	33332 88783
sgggggg dddd ssss	sgggddgggggsggg ddddddddd ddd sssssssss sss	ggggsgggggsgs dddd dddd d ssss ssss s	ssddddgddsdddddsddmddgdssdddssssdsgggsdd ddds ds sssgs ssdssdsdddssddddsdddddd sss s s s s sss ssss sssssss	sgssssgmggggsg d dddddd d s ssssss s	sssddsssgdd dddssdddddd sss ssssss	ssssssssss tttttttttt	ssssssssgsttg ttttttttd s	ttttt	dtsdt d d s s
ssddsss d	sssdddsdsdddsss dd	sddddsssssssd dddds	ddaasdsssasssssasssssadsassasssssssssssass l dd l l al lsal hdd l l hl a l	sssssdsssddsdd d dd aa haa ll all l	ssssssssssas dddd h dlh	ssdssssssd ds ddddds h h	dsssssdsgddss d ddh dd d	sssss dddhh d	aasad lldl
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3111111	111131111111222	5111111111412	5133221333111113142122111321133121111122	22115441115121	32542333335	5422211211	2111132112421	24332	32131
SNNSWN0 WE	NNENNSS00NN0000 E E WW	NNSNNN0N0NNNS EEWW W W W	000N00WE0000000N00000W000000000000000000	NN000N0S000000 E	NNNN000000N	S0WSNSNS0S E E	SSNNWNN0SNS0N W EN W W	NNNNE W	0000N
1 2 3284000	1 200643200960000	 2065040402805	2 0000000200000055200002000000000000000000	 25002204000000	 00110000000	11 8055242204	1 1 1 1 3936533024103	11 46332	 20003
3444444 0444444 8444446	444344444444444 444144444444444 444644444444444	344444444434 0444444444142 9444444444627	33333344333333 2222133 322223333 33 1111104410000011112746437142844490298 11 060027243777765113052773653520097951 33	34333 1112233 04000119997700 84777482923477	33333223333 00004430000 77776217777	3333333223 2640112532 8828668018	3333333332223 2211041447788 8866826253552	33333 00004 77770	33324 21161 70281
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nnnnnny	nnnnnnnnnnnnnnn	nnnnnnnnnnnnn	nnnnnnnnnnnnnnnnnnnnnnnnynnnnnnnnnnyyyynnnn	nnnnnnnnnnnnnn	nnnnnnnnnnn	nnnynnnnnn	nnnnnnnnnnnnnn	nnnnn	nnnnn
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3162315 0005050	22 212 1 666 500000050055000	44533422111 0000000505555	2 3 51 13 4 0000000050000000555000000000000000500000	1 1 3 50560000000000	7 14 53500000200	3 482222 0000000000	22435 4853 0005000000000	3331 05000	 00000
1112221 3230117	11111 11111111 241564525324203	111 11 11 4593996981735	1 1111211111 1121221111 2 112121 7698662396660521526312813537982983241778	2 321212111111 79188171584844	21221 11211 29049805064	1111 2 2 1 3740959357	1112121221221 1270221507511	1112 68440	112 07740

and

Geology		Landform		Erosion Index		Aspect		Soil Type	
d	dolerite	cs	convex slope	1	O-horizon intact	N	north	mrc	Mispah-rock complex
s	sandstone	co	concave slope	2	O-horizon absent	NNE	north-north-east	m	Mispah form
sh	mudstone	p	pediment	3	Initial erosion of A-horizon	NE	north-east	mnd	Mispah-Nyoka-Dudfield
l	lidianite	pl	plateau	4	Moderate erosion of A-horizon and pedestal formation	E	east	sli	sandy lithosol
al	alluvium	b	bottomland	5	excessive erosion of A-horizon with plinthite exposed	ESE	east-south-east	sw	Swartland Form
		rr	rocky ridge			S	south	al	alluvium
						W	west	c	colluvium
						WNW	west-north-west		
						NW	north-west		
						0	flat, with no specific aspect		

APPENDIX 2. Site environmental variables on quadrats surveyed in the Camdebo and Sneeuberg region

Community Number	IA1	IA2	IB1	IIA1	IIA2	IIA3	IIA4	IIA5	IIIA1	
Quadrat Number	212 797 445	2222 7772 0230	211122222222 499211371234 913589387341	1211 88999999711 35147899167	1112 2224 1233	111 99112 56344	1111122211122 88899900459933 48907801405689	1112222221111111 2461233441334556 9970212675093190	11111111111111 022333333444555 378145678012345	1111 93344 22345
Altitude (m)	11 753 058 013	1111 3666 4363 8976	111111111111 736535643444 054598009452 000000000000	1 11 11111 17721133333 22314202130 07000000000	1111 2336 7336 0000	11111 32234 34135 02000	11111111111 23333333433379 16662500836680 00000000000000	111 111111111111 0034612333000000 1132204303811111 0000000000000000	11111111111111 900000000000000 792840021111414 000000000000500	11111 10000 42811 20000
Veld Type	244 224	3666 7000	664666666666 002000000000	33333333363 76777777707	3666 7000	33663 77007	33333333323366 77777777657708	3333333446333333 7777767220777777	233333333333333 577777777777777	33333 77777
Formation	gmm dg s	smsm d d s s	mmmmmdsmmmmm dddggm ggdgg sss d s s	tdsgsssmsss d d s s s	dgdm ddsg ss	sdmms mdd gss	ssssgssdgggggg s d s	gggsdgsmdsgggggg dd dd ds dddd ss ss ss ssss	sggddgggggsggg ddddddddd ddd sssssssss sss	ggggs dddd ssss
Geology	sdd	dsds hd	sssddsdssdds h a	sassssldss dld dddd dd	sdss s	sssds dddd	dsssddsdssddss dd lldl d h	dsddddssssddsss d d	sssdddsdsdddsss dd	sdddd
Landform	pcc os	ppca llsl	cccpcccccrpp ssslossssrl	cbcbccccpcc o s sssolss	cccc osss	cccpc sssls	cccccccpcccpp soossso sssll	ccpccpcccccccpp sslss sssossss	ccpcrcccpccpppp ss srsss ss	cpprr sllrr
Erosion Index	111	1113	111114111121	25143333311	3141	22111	11111133321111	111333223311111	111131111111222	51111
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Veld Type (Acocks 1975)
22 Invasion of Grassveld by *Acacia karroo*
24 Noorsveld
25 Succulent Mountain Scrub (Spekboomveld)
36 False Upper Karoo
37 False Karroid Broken Veld
38 False Central Lower Karoo
42 Karroid *Merxmuellera* Mountain Veld replaced by karoo
44 Highland Sourveld and Dohne Sourveld
60 Karroid *Merxmuellera* Mountain Veld
68 Eastern Province Grassveld

Formation (field assessment)
ds Dwarf Shrubland
gds Grassy Dwarf Shrubland
sds Succulent Dwarf Shrubland
dds Degraded Dwarf Shrubland
mds Montane Dwarf Shrubland
dmds Degraded Montane Dwarf Shrubland
s Shrubland
t Thicket
st Succulent Thicket
g Grassland
mg Montane Grassland
dmg Degraded Montane Grassland

Geology
d dolerite
s sandstone
sh mudstone
l lidianite
al alluvium

Landform
cs conve
co conca
p pedim
pl plate
b botto
rr rocky

000 SOUTH AFRICA SUID-AFRIKA

A

LANDSAT SAMPLING UNITS

3224 GRAAFF-REINET

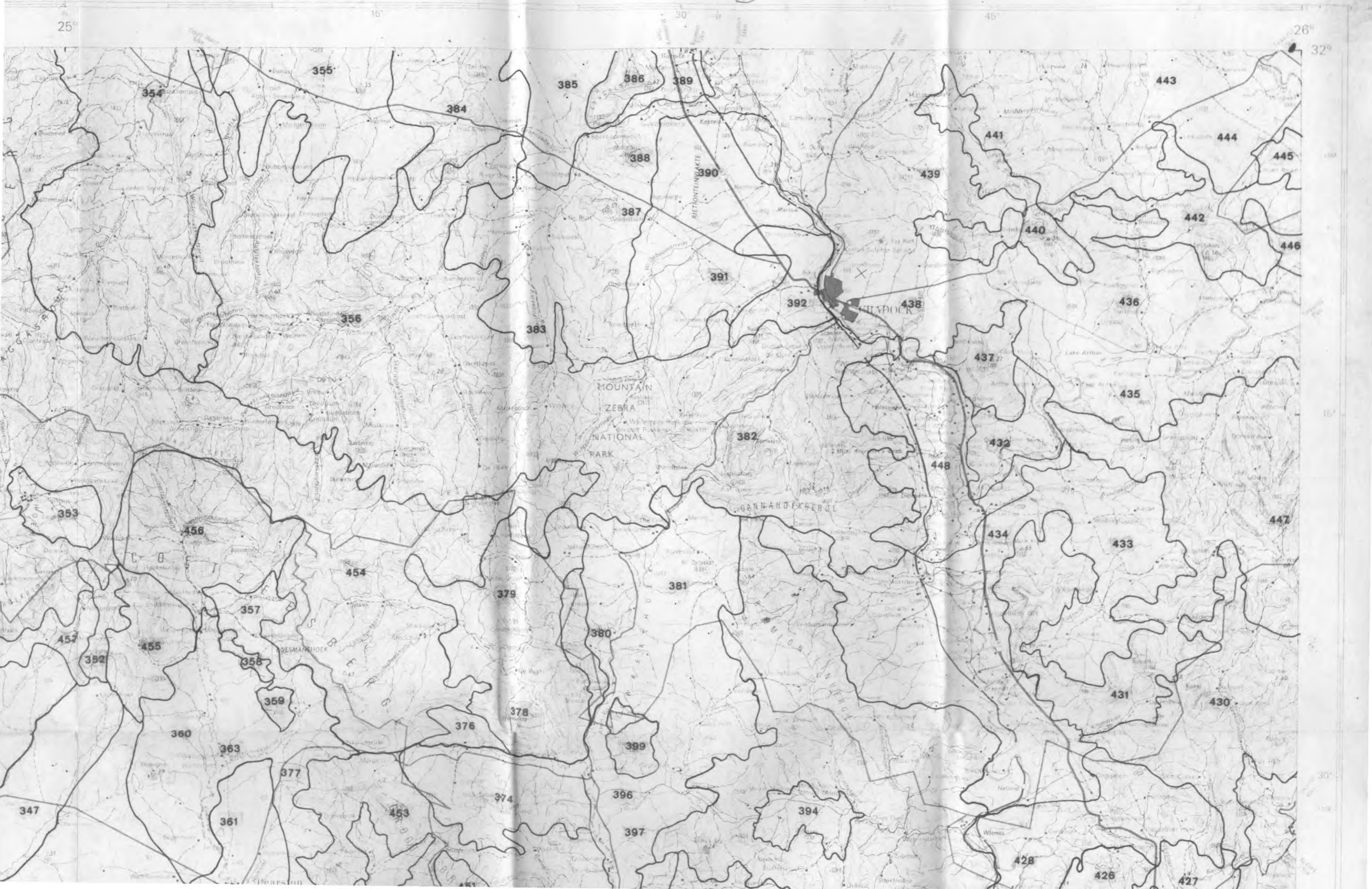
T SAMPLING UNITS

RAAFF-REINET

Refer to this Map as SOUTH AFRICA 1:250 000 TOPO-CADASTRAL Sheet
Verwys na hierdie Kaart as SUID-AFRIKA 1:250 000 TOPO-KADASTRALE Vel

3224 GRAAFF-REINET

B



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Cookhouse
Uitkeer
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