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

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A phytosociological survey according to the approach and methods of the Zürich–Montpeillier 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.

'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 plato's, word beskryf. 'n Hiërargiese 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 en 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: Dwarf Shrublands, semi-arid, 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:

(a) To prepare an inventory of the plant communities of the nature reserve;
(b) to classify these communities using the Braun–Blanquet technique;
(c) 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.

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

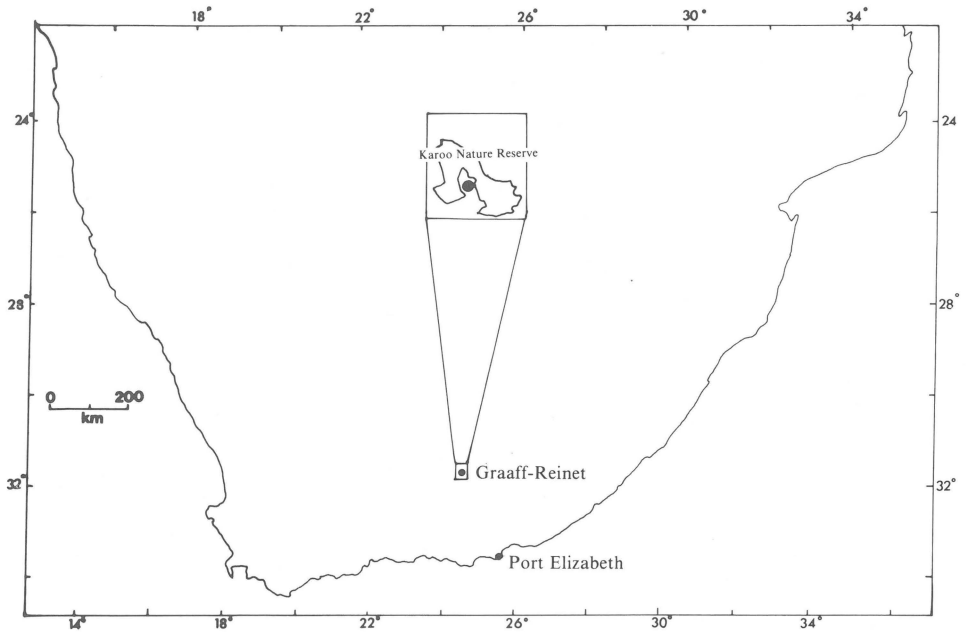

Figure 1 The location of the study area.

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 sandtone (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

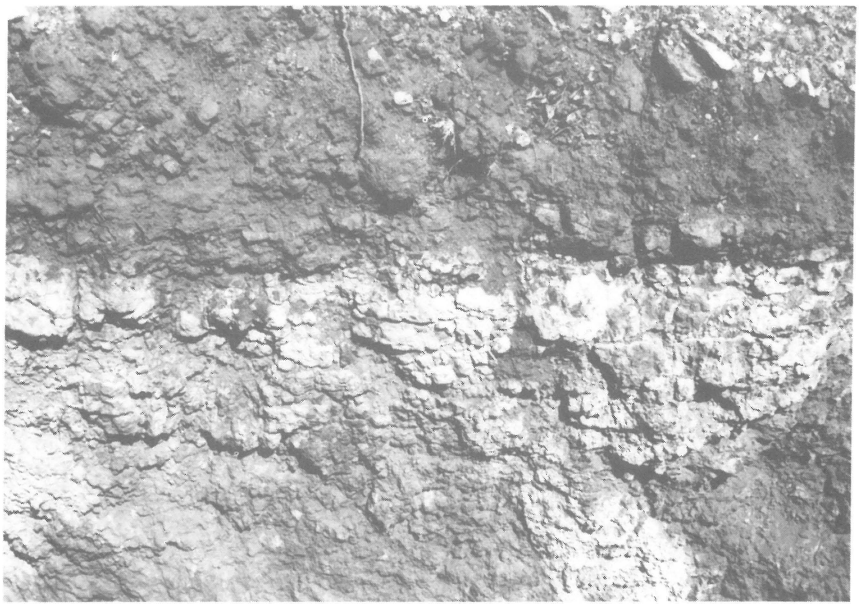

Figure 2 The white calcareous hardpan in a soil profile on the Karoo Nature Reserve. The hardpan is encountered at approximately 30 cm below the surface of the pediments throughout the Camdebo plain. Roots, obvious in the upper half of the photograph, are seldom found below this layer.

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

(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 23 m 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 (< 120 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 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). Fog occurs frequently over the high-lying areas, predominantly from February to April, and contributes 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).

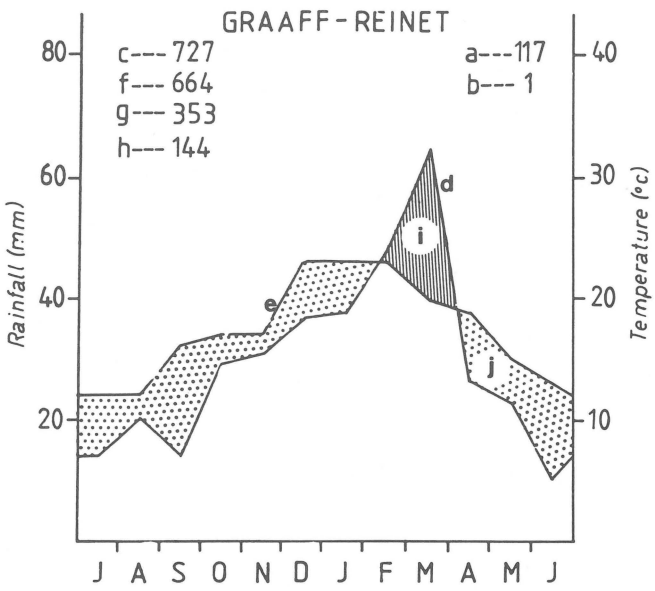

Figure 4 A Walter–Lieth climate diagram for Graaff-Reinet. (a) Number of recording years (rainfall); (b) number of recording years (temperature); (c) altitude; (d) curve of mean monthly rainfall; (e) curve of mean monthly temperature; (f) highest annual precipitation (mm); (g) mean annual precipitation (mm); (h) lowest annual precipitation (mm); (i) wet season; (j) dry season.

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 12 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 × 10 m were selected throughout the study area (Figure 5). A plot size of 10 m × 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 × 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 × 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

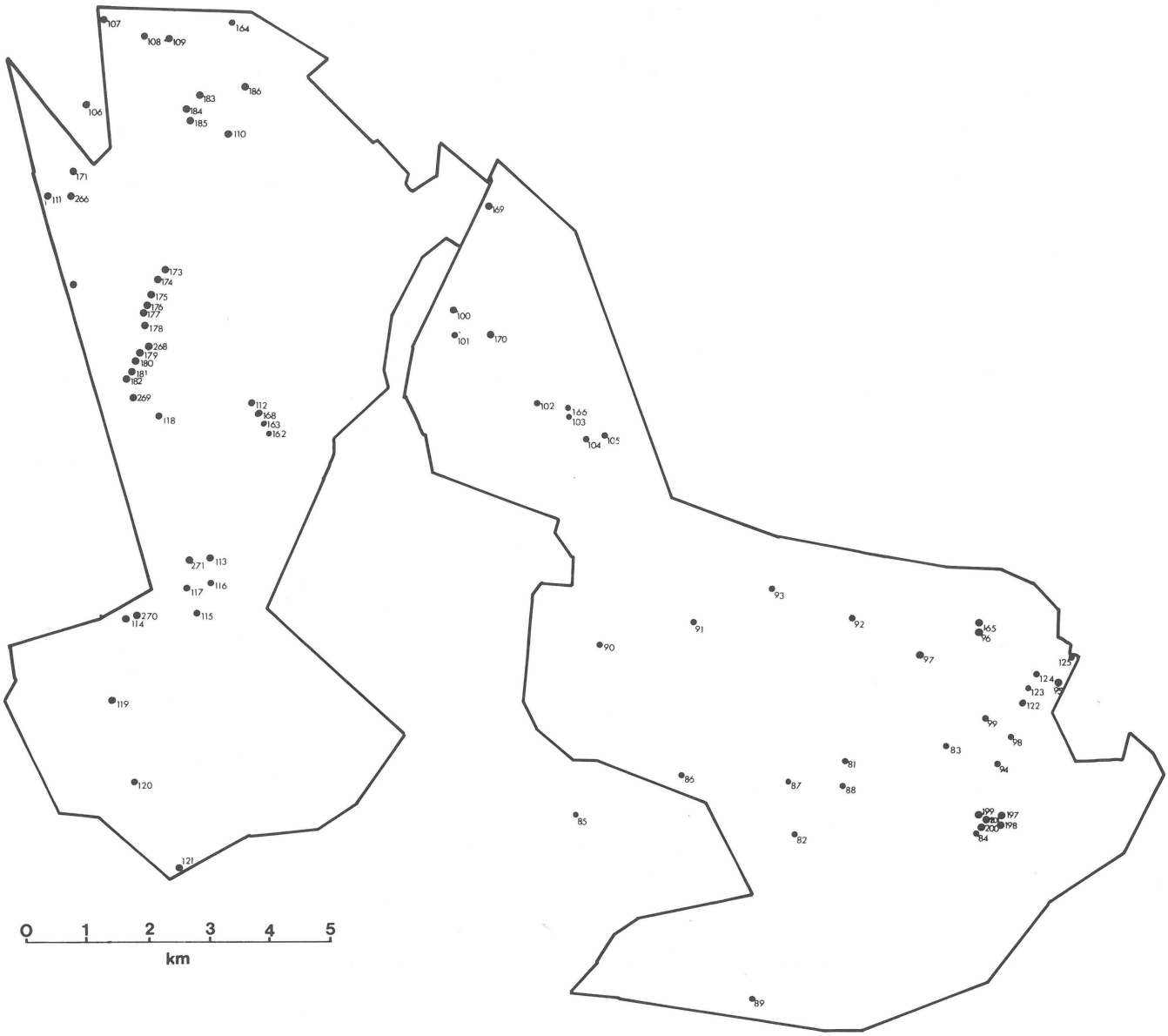

Figure 5 The distribution of relevés surveyed on the Karoo Nature Reserve.

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 1989a). The cover-abundance values applied were those recommended by Barkman *et al.* (1964). Rearrangement 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.

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				
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

Table 1 Continued

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
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
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				

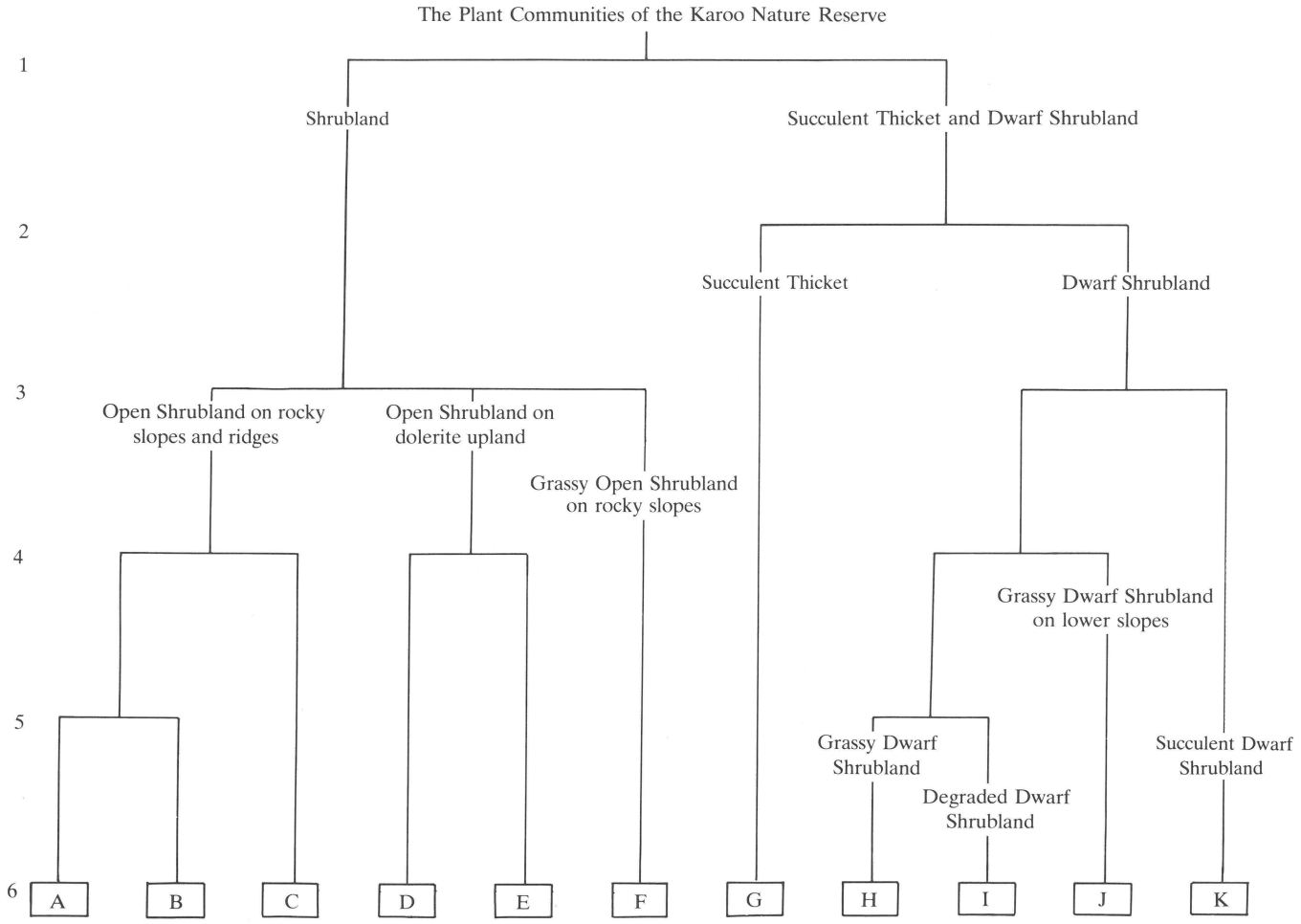

Figure 6 The hierarchical classification of the vegetation of the Karoo Nature Reserve. This was achieved after slight modification of the result of a TWINSPAN tabulation.

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 15 or more species. This phenomenon was recorded previously by Martin & Noel (1960) in the Albany and Bathurst districts and Palmer (1981) in the subtropical 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 inter-clump cover. When dwarf shrubs are the dominant inter-clump 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 subdivided 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 1 000 and 1 300 m above sea level. The soils are part of the Mispak-rock complex in which a shallow (20–60 cm) A-horizon covers rocky parent material. Large rocks and boulders (dolerite and lidianite) occur in the soil profile, and lead to an underestimate of soil depth. The soils are deeper than expected, and woody shrubs can penetrate to a depth of 3 or 4 m. This was evidenced by visible root penetration in cuttings and gullies.

The most prominent shrub is *Rhus undulata* which

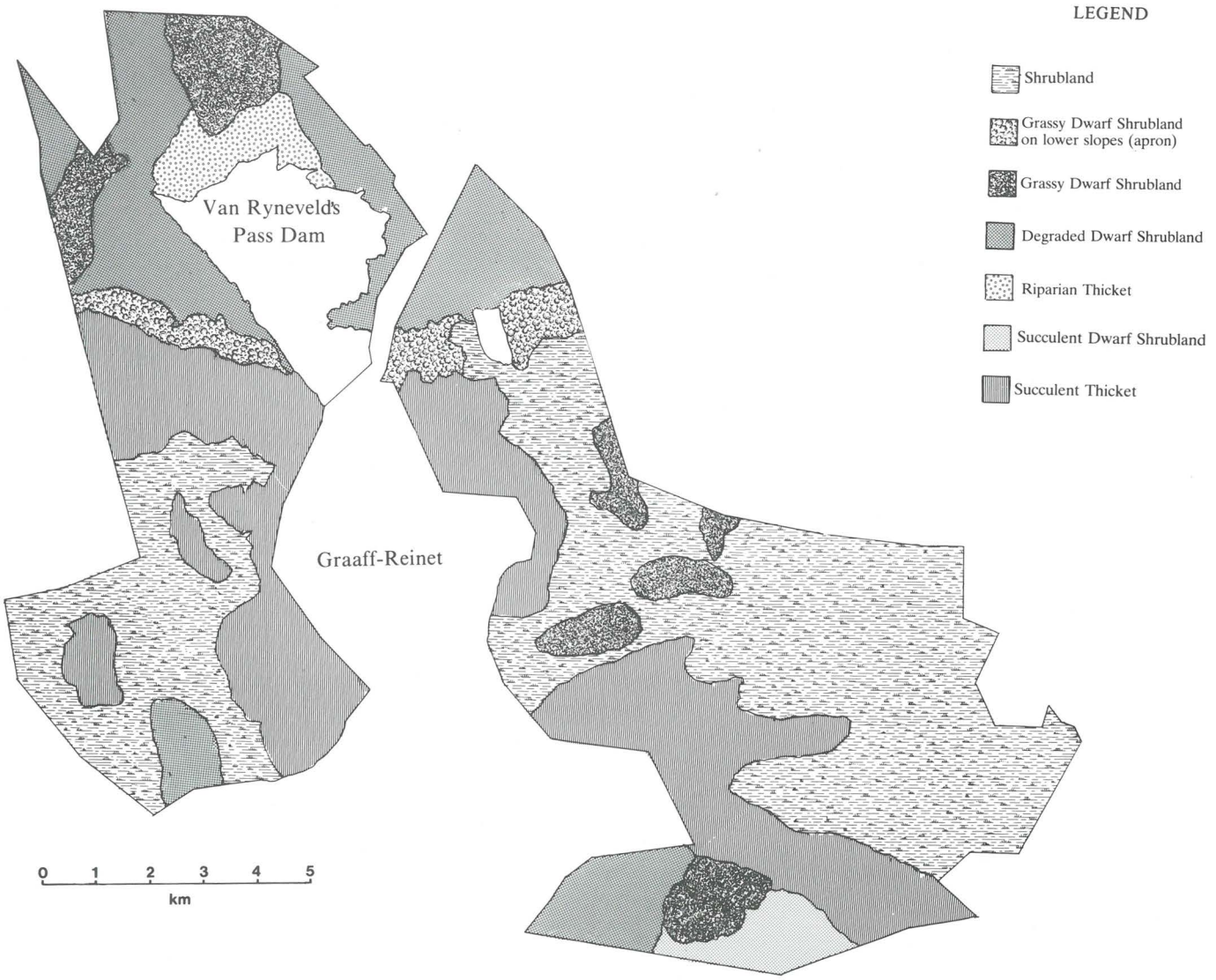

Figure 7 The vegetation map of the Karoo Nature Reserve.

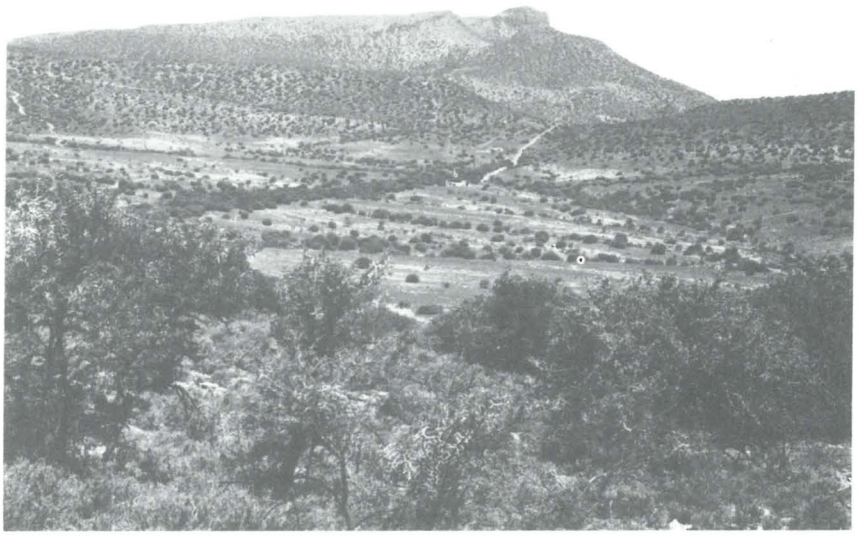

Figure 8 The Shrublands of the rocky slopes and ridges of the Karoo Nature Reserve. Shrublands consist of clumps of woody species, *Rhus undulata, Maytenus polyacantha, Euclea undulata* and *Acacia karroo,* interspersed by Dwarf Shrubland or Grassland.

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

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* subsp. *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 Edwards's (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,

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.*

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, dorsoventrally differentiated and evergreen. These may be adaptations to the low temperatures and regular snowfalls which occur in the uplands during winter. The interclump 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 austroafricana, 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 50 cm and more. The low clay content of the soil means that water-logging 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 1989b). 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 (*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*

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

striatus, and grasses, including *Aristida congesta* (both subspp.), *Tragus koelerioides, Eragrostis lemanniana* 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° and 3°, and seldom reaches 7° (Fair 1948). The drainage lines may have developed into pronounced erosion gullies, cutting down 4 to 5 m into the friable alluvium until reaching bedrock.

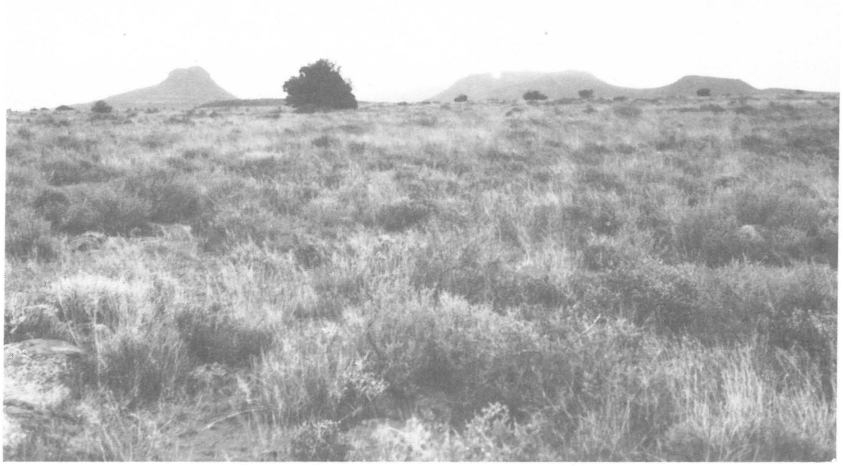

Figure 12 Grassy Dwarf Shrubland on Waaierstertplaat, Karoo Nature Reserve, with an indication of the visual contribution which the grass genera *Eragrostis, Aristida, Tragus,* and *Sporobolus* make to the composition of the landscape.

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 5 cm 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.* (1986) 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 1989b). 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^{-1}.)

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. *Geigertia 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 Rhyneveld's 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

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

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 subtropical, and I recognized two strong associations which occur in Valley Bushveld, Noorsveld and Spekboomveld, namely the *Portulacaria afra–Pappea capensis* association, and the *Euphorbia bothae–Rhigozum obovatum* association (Palmer 1981). It is the integrity of these associations which leads 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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