The physical environment and major plant communities of the Karoo National Park, South Africa

FRANCINE RUBIN and A.R. PALMER

Rubin, Francine and A.R. Palmer. 1996. The physical environment and major plant communities of the Karoo National Park, South Africa. *Koedoe* 39(2): 25-52. Pretoria. ISSN 0075-6458.

The major plant communities of the Karoo National Park are described using the methods of the Zürich-Montpellier school of phytosociology, to assist with the formulation of a management strategy for the park. The vegetation physiognomy consists of Montane Karoo grassy shrublands, Karoo grassy dwarf shrublands, Karoo succulent dwarf shrublands and riparian thicket. Steep elevation and precipitation gradients within the study area have a direct impact on gradients in the vegetation. High elevation (1 800 m), and relatively high rainfall (406 mm) montane grasslands occupy communities dominated by grasses (*Merxmuellera disticha*, *Themeda triandra*) and woody species (*Diospyros austro-africana*, *Elytropappus rhinocerotis*, *Euryops annae*, *Passerina montana*). The increasing aridity away from the escarpment edge in a northerly direction is steep, and Montane Karoo dwarf shrublands replace these mesic communities. Species such as *Eriocephalus ericoides*, *Rosenia oppositifolia* and *Pteronia tricephala* dominate. At lower elevation (800 m) the precipitation is very low (175 mm) and uncertain (coefficient of variation of 78 %). The substrata influence the vegetation, with the sandy substrata of the drainage lines supporting more woody taxa (*Acacia karroo*, *Lycium cinereum*) and grasses (*Hyparrhenia hirta*, *Stipagrostis namaquensis*, *Cenchrus ciliaris*). Moving away from the mesic environment of the riparian zone, rapid desiccation occurs and the most xeric communities are encountered, dominated by *Stipagrostis obtusa*, *S. ciliata* and *Pentzia incana*. This document provides descriptions of the general communities and their associated landscape, lithology and soils.

Keywords: phytosociology, semi-arid, Karoo.

Francine Rubin, National Parks Board, P.O. Box 176, Sedgefield, 6573 Republic of South Africa; A.R. Palmer, ARC Range and Forage Institute, P.O. Box 101, Grahamstown, 6140 Republic of South Africa.

Introduction

An important function of a national park is to protect the ecological integrity of one or more ecosystems for present and future generations (Green 1993). The urge to conserve the Karoo in the mid 1970s followed an International Union for the Conservation Nature and Natural Resources meeting at the time when their Council for National Parks and Protected Areas Committee was initiated. The South African Nature Foundation purchased two pieces of land with the help of a national fund raising effort. Two conservation areas were established virtually simultaneously, one surrounding the town of Graaff-Reinet (Karoo Nature Reserve) and the other near Beaufort West (Karoo National Park).

Vegetation changes are seldom accurately predicted because of their dependence on multiple variables (Burrows 1990). However, change in plant species composition in the Karoo and other semi-arid rangeland areas throughout the world, due to livestock farming practices, have been widely described (Acocks 1953; Noy-Meir 1982; Roux & Vorster 1983, Schofield & Bucher 1986; Le

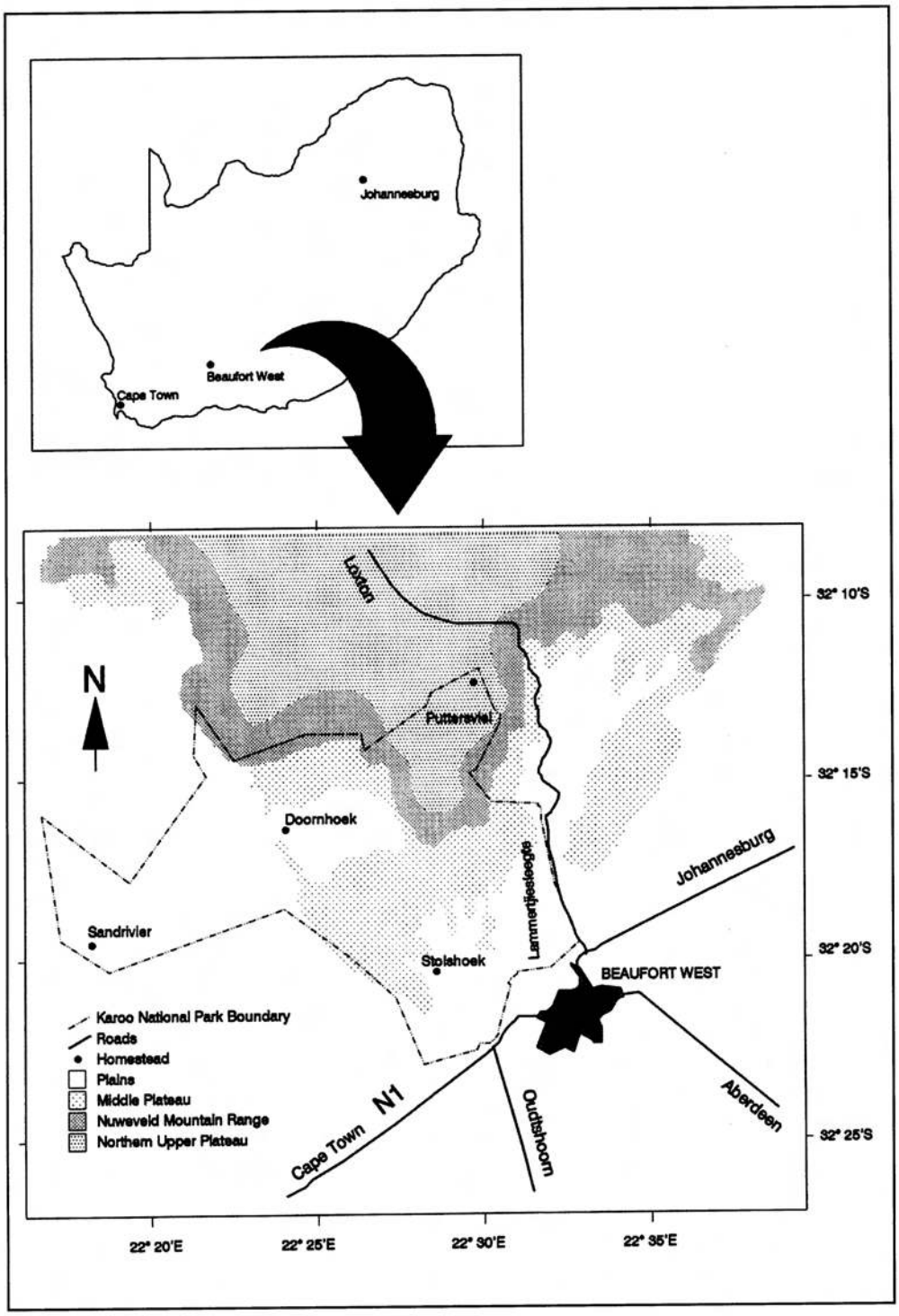


Fig. 1. Map showing the locality, dominant topography and principle areas within the Karoo National Park.

Houérou 1989; Moore 1989; Westoby *et al.* 1989; Friedel *et al.* 1990; Hoffman & Cowling 1990; Bosch & Booysen 1992; Taylor & Ralphs 1992). Prior to the establishment of a national park at Beaufort West, this area was utilised extensively for the purpose of small stock farming. The Karoo National Park (KRNP) could serve as a benchmark site for future comparisons with similar regions, and to determine the change in vegetation composition after the termination of stock farming. A phytosociological study will be a baseline inventory of the plant communities of the park and their related environmental properties. This would assist in the monitoring of botanical diversity, and provide guidelines for the environmental management of the park.

This study therefore describes the vegetation of the Karoo National Park following on descriptions of the Karoo Nature Reserve (Palmer 1989, 1991a, 1991b).

Study Area

The KRNP is situated due west to northwest of Beaufort West against the Nuweveld Mountain range at 32°11'S–32°23'S and 22°15'E–22°35'E (Fig.1). The Town Council of Beaufort West donated 7 209 ha of communal land (Lammertjiesleegte) northwest of Beaufort West to the National Parks Board (NPB). This formed the nucleus of the KRNP, proclaimed in 1979. Additional land purchased included the farms: De Kamp, Stolshoek, Puttersvlei, Doornhoek, Sandrivier and the northern part of the communal land. Together these farms comprised approximately 33 000 ha, and are the only sections included in this study. Expansion of the KRNP continues through acquisition of land and is at present exceeding 46 000 ha.

Geomorphology and physiography

The macro-scale landscape extends from the Great Karoo, across the mountains of the Great Escarpment to the Upper Karoo (King 1942), or Southern Interior Basin (Kruger 1983). Landform (Fig. 2) establishes a moisture gradient (Knight 1987), with arid conditions at low elevation changing rapidly to high rainfall mesic conditions at the higher altitudes, 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 plains or pediments. These areas are never completely flat, and drainage lines or erosion gullies generally transverse, incised into the structureless Quaternary alluvium. Lower pediments may contain shallow pans (Gabriel & Talbot 1984) where sodium, calcium and magnesium carbonates, and phosphate, have accumulated.

The KRNP divides into four physiographic units (Fig.1): the southern and western plains (<1 200 m); the middle plateau (1 200-1 300 m); the mountain range (>1 300-1 900 m) and the northern upper plateau (1 600-1 900 m) (Fig. 2). The southern plains are part of a large interior basin overlying resistant rocks, upon which deep, alluvial soils have been deposited or have developed *in situ* (Johnson & Keyser 1979). The southern and western plains include Sandrivier, Doornhoek basin, Stolshoek and Lammertjiesleegte, and contain raised flat sandstone pavements, with sharp mudstone slopes.

The middle plateau consists of flat, rocky pavements, rocky outcrops from dolerite dykes and sandy pediments. Cliffs, steep scree-covered slopes and incised gorges are common along the mountain range. A gently undulating rocky landscape and flat sandstone terraces are found on the northern upper plateau (Puttersvlei).

Significant water catchment occurs along the steep escarpment area. Advective fog and cloud accumulate on its southern aspect, and light precipitation often extends over the edge for a few kilometres. This results in an aridity gradient extending away from the escarpment in a northerly direction.

Geology

The Karoo Supergroup of Permian age consists of the Dwyka Formation, Ecca Group and Beaufort Group (Johnson & Keyser 1979). The Beaufort Group overlies the Ecca Group and consists of alternating mudstone (red in places) and sandstone. It sub-divides into a lower Abrahamskraal Formation (1500-2000 m thick) and an upper Teekloof Formation (‡ 1400 m thick) with the boundary arbitrarily at the base of the so-called "Poortjie Sandstone" (Johnson & Keyser 1979). The Abrahamskraal Formation is exposed in the Doornhoek and Sandrivier basins. This formation consists of mudstone (red in places), sandstone and thin, greenish cherty beds (Geological Map Beaufort West 1:250 000). The sandstones represent river-channel deposits and the mudstones, floodplain

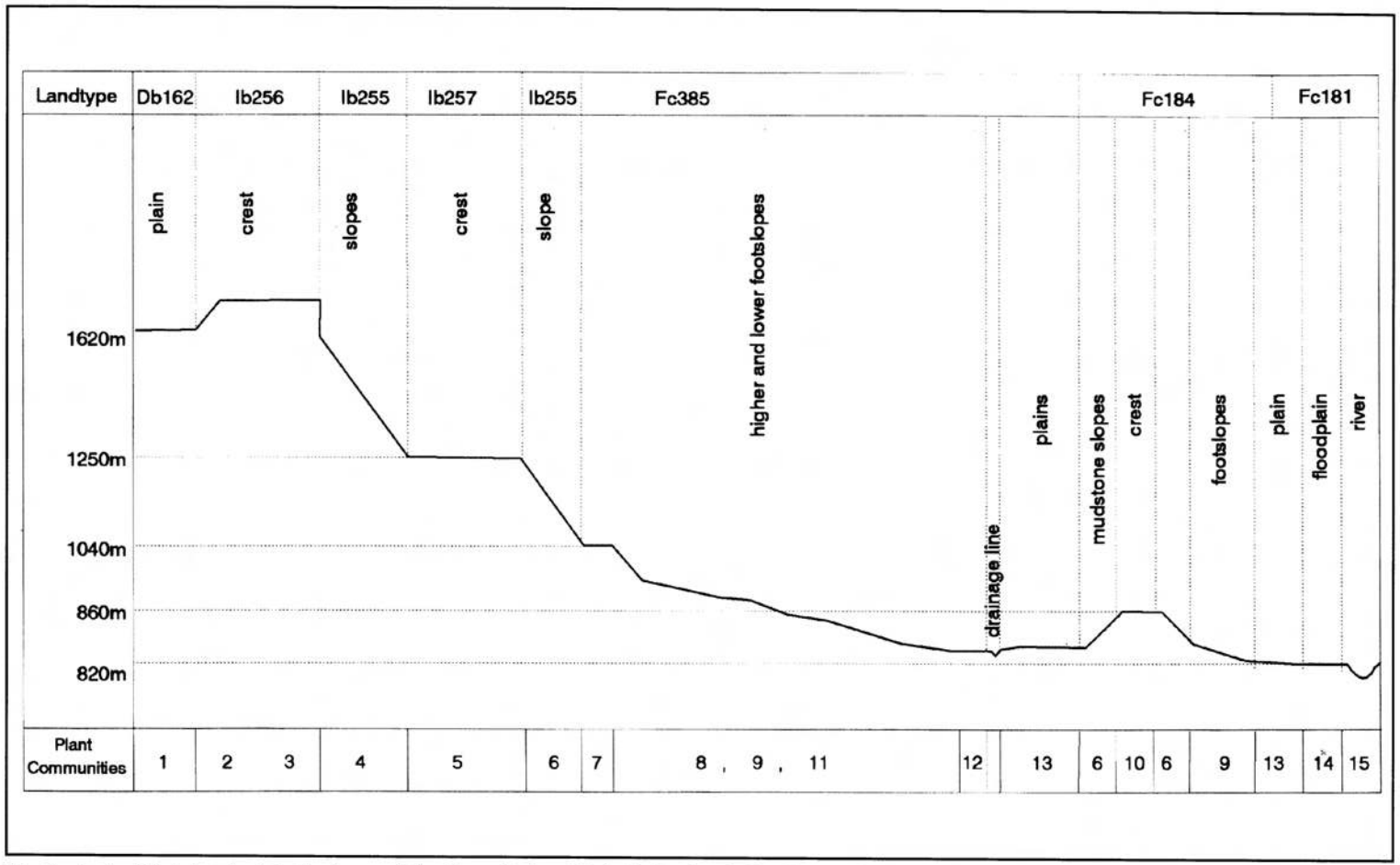


Fig. 2. A simplified sketch of the landscape of the Karoo National Park, indicating the Land type units (Land Type Survey Staff, 1993), topographical position and plant communities.

ISSN 0075-6458

deposits (Johnson & Keyser 1979). The cherty beds were originally ashfall tuffs, although the presence of micro-cross-lamination suggests subsequent transportation by water onto the floodplains (Johnson & Keyser 1979).

A greater relative abundance of red mudstone and fewer cherty beds characterises the Teekloof Formation, compared to the similar (i.e. mudstone and sandstone) Abrahamskraal formation (Johnson & Keyser 1979). The formation is exposed on the upper slopes of the Doornhoek basin, the slopes of Stolshoek, Lammertjiesleegte and the slopes of the middle plateau.

Jurassic-age dolerite extensively intrudes the Beaufort Group as dykes and sheets. Inclined sheets form crescent-shaped or concentric intrusions that are clearly visible on the middle and upper plateau. The sills range from a few metres to over 100 m in thickness. The dolerite causes a metamorphosis effect on the adjacent host rocks. Mudstones altered to hornfels and the sandstones develop a quartzitic appearance (Johnson & Keyser 1979).

Deposits of Quaternary age include river terrace gravel, calcrete, alluvium and debris. Terrace gravel consists of fairly well- rounded cobbles and boulders composed largely of dolerite (Johnson & Keyser 1979). The terrace gravel shows clearly along the banks of the Gamka River where sharp profiles occur. These gravels are partly calcrete cemented and occur on terrace remnants that now lie a few metres—to a maximum of 30 m—above the general land surface. Calcrete occurs directly on bedrock and also formed extensive deposits within some larger areas of alluvium, and may attain a maximum thickness of a few metres. The alluvium embraces both alluvial slopes (sheet wash) and alluvial valley (channel-related) deposits (Johnson & Keyser 1979), with the former predominating in Lammertjiesleegte and the latter dominating in Stolshoek.

Land type mapping and soils

Three major land types, the Fc, Ib, and Db (Land Type Survey Staff 1993) occur in the Karoo National Park (Fig. 2). The Fc land type occurs in the entire Sandrivier, Lammertjiesleegte, the low-lying areas of Doornhoek, and the Stolshoek section of the study area. This land type holds pedologically young landscapes that are not predominantly alluvial or aeolian. The dominant soil-forming processes have been rock weathering, the formation of orthic topsoil horizons and, commonly, clay illuviation, giving rise typically to lithucutanic horizons. Soil forms that are typical of these processes are Glenrosa and Mispah. Any other soil form can however also be found in these land types. Oakleaf soil forms, deep or shallow, developed by rock weathering also occur in upland sites. Fc refers to soils where lime is common in upland and valley bottom areas (Land Type Survey Staff 1993). The lime suggests the extent to which leaching has taken place. In localised areas landscapes are found with accumulation of soluble salts instead of lime.

The steep slopes, middle plateau and Puttersvlei (upper plateau), excluding the northern most corner, fall into the Ib land type. Surface rock with underlying soil or rock covers sixty to eighty percent of these areas. The parent material of the slopes consists of mudstone, siltstone and sandstone with some dolerite intrusions, and typically Glenrosa and Mispah soil forms. Dolerite covers most of the middle plateau, with an influence of mudstone, siltstone and sandstone closer to the upper slopes (Land Type Survey Staff 1993). Fertile soils occur on this flat plateau (Greyling 1989), with little erosion save where the deep red soils gradually erode from a natural basin. Dolerite rocks cover most of the Puttersvlei section of land type Ib, with the underlying sandstone appearing in terraces, descending in a northerly direction.

The northernmost corner of the upper plateau occurs in land type Db. Prismacutanic and/or pedocutanic diagnostic horizons characteristically dominate this land type. Non-red B horizon, duplex soils cover more than half the area (Land Type Survey Staff 1993).

Climate

Mean annual precipitation ranges from 175 mm at Sandrivier (Karoo National Park *pers. comm.*), 254 mm at Stolshoek, 239 mm at Beaufort West to 406 mm at Puttersvlei (Dent *et al.* 1987) (Fig. 3). Rainfall reliability, as expressed by the coefficient of variation in annual rainfall, diminishes from west to east. Sixty to seventy percent of the mean annual precipitation falls in summer (October to March). The mean July minimum temperature is 3.5 °C and mean January maximum temperature is >32 °C. The mountains of the Great Escarpment experience a cool steppe climate (Schulze 1947), with the steep elevation and precipitation gradient rapidly changing to a warm steppe climate in the eastern, southern and western lowlands (Vorster 1985a).

Biogeographical affinity

Werger (1978a) and White (1983) regard the extensive arid and semi-arid areas of the south-western

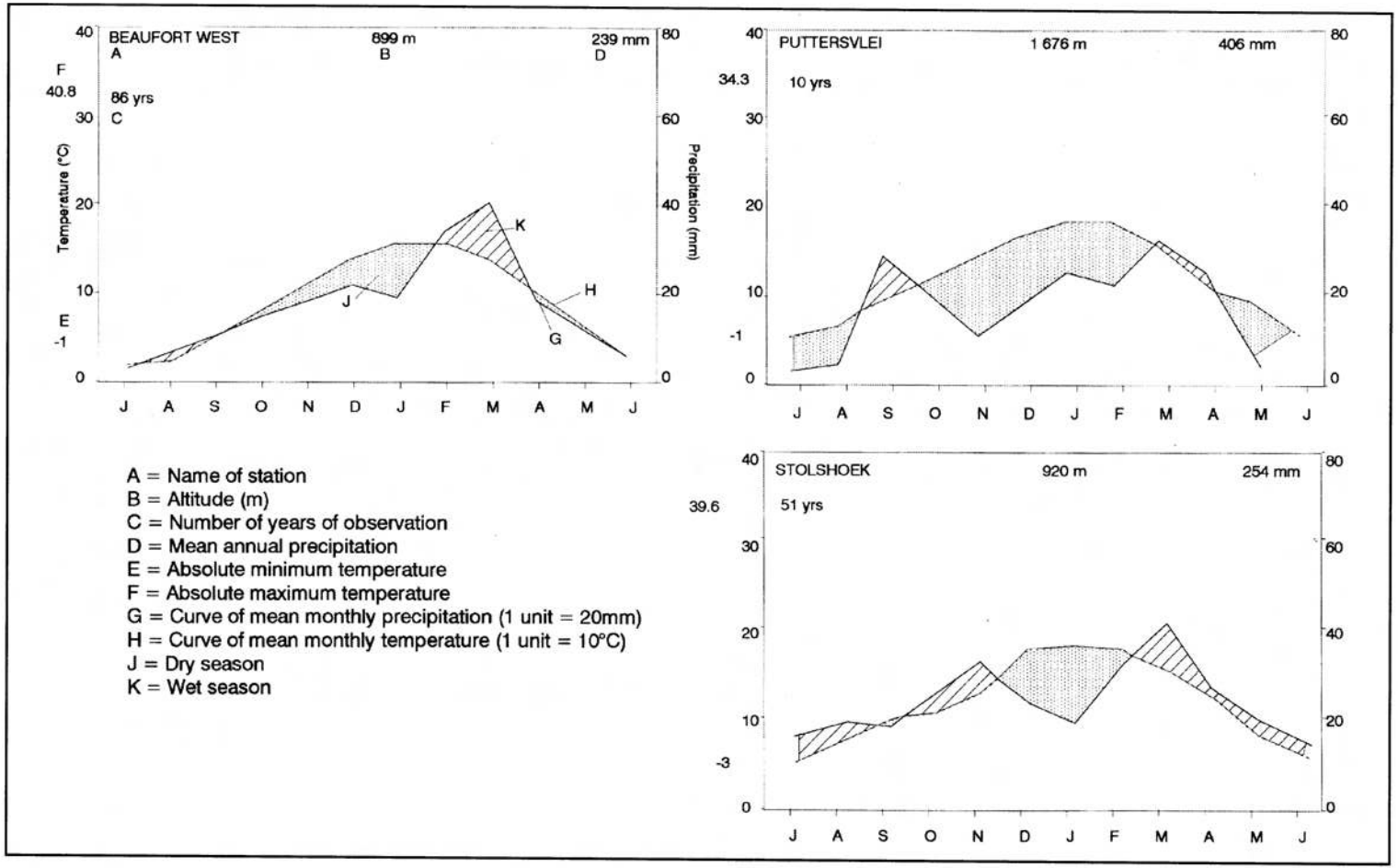


Fig. 3. Climate diagrams for Stolshoek, Puttersvlei and Beaufort West (diagrams according to Walther & Lieth (1960)).

ISSN 0075-6458

part of southern Africa as the Karoo-Namib biogeographical region. White (1983) defines three major vegetation types in the study area, namely bushland and thicket, semi-desert vegetation and grassy shrubland. Bushland and thicket contain one subdivision, 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.

Three biomes divide the Karoo-Namib region (Rutherford & Westfall 1986), namely the Nama-Karoo Biome, the Succulent Karoo Biome and the Desert Biome. According to this classification, this study area falls completely within the Nama-Karoo Biome.

Four phytochorological regions meet in the study area. These are the Tongaland-Pondoland succulent thickets (Moll & White 1978), Karoo-Namib elements (Werger 1978b), Afro-montane remnants (White 1983), 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, contributed to the vegetation patterns.

The three veld types (Acocks 1988) in the study area are Karroid Broken Veld of the Great Karoo (VT 26), Central Lower Karoo (VT 30) and Karroid Merxmuellera Mountain Veld replaced by Karoo vegetation (VT 42).

Methods

This study applied methods and techniques of the Zürich-Montpellier school (Westhoff & Van der Maarel 1973; Mueller-Dombois & Ellenberg 1974; Werger 1974). Stratified random sampling (Southwood 1978) was used to select 157 sampling sites. Stratification of aerial photographs, topographical position, aspect and geology divided the study area into sampling units. Plot sizes were approximately 10 m x 10 m (Palmer 1989). In each sample plot, all species were recorded, a percentage projected canopy cover was estimated subjectively for each plant and cover-abundance values were allocated according to the scale of Barkman *et al.* (1964). Common but sparse species in a plant community, were often given the value of R because of rarity within the sampling plot. Voucher specimens were submitted to the National Botanical Institute in Pretoria, and the Selmar Schonland Herbarium in Grahamstown, and taxon names conform to those of Arnold & De Wet (1993). Environmental variables such as slope, aspect, geology, rockiness of soil surface, erosion and degree of utilisation by herbivores were recorded in each sample plot (Van Rooyen 1978; Schmidt 1992) and summarised for each community after completion of the phytosociological classification.

Two-way indicator species analysis (TWINSPAN) (Hill 1979) was applied to the floristic data set to derive a first approximation of the plant communities of the park. The data was refined with Braun-Blanquet procedures (Fuls *et al.* 1993; Eckhardt *et al.* 1993; Bezuidenhout 1994) using manual tabulation on a spreadsheet, and 15 major plant communities were identified. Three sampling sites fell into specialised plant communities (40, 57 and 63), and were excluded from the final phytosociological table.

In quadrats along the topo-moisture gradient, soil samples were collected. These were later analysed for pH (KCl), Na, Al, Ca, Mg, K, total P, sand, soil texture, cation exchange capacity and organic carbon, following the methods of the FSSA (1974).

A global positioning system recorded the location (dd:mm:ss) of every sample site. A SPOT High Resolution Visible image was purchased and rectified to a latitude-longitude grid using the GRASS4.0 GIS. Radiometric data for each sample, in all three bands, were extracted. These data, combined with elevation, rainfall, substrate and soil data, assisted in identifying mappable units of vegetation. Mean annual precipitation from Dent *et al.* (1987) were used to determine the rainfall for the main geographical regions.

Results and discussion

A summary of the vegetation classification and most prominent determining factors are (see Table 1 and Figs. 2 & 5):

1. The *Eriocephalus ericoides - Pteronia tricephala* Montane Dwarf Shrubland of the duplex soils, on the most northern plain of the Puttersvlei section.

2. The *Merxmuellera disticha - Lightfootia nodosa* Montane Grassland on the rocky slopes of the Puttersvlei section.

3. The *Euryops annae - Elytropappus rhinocerotis*

Montane Shrubland of the alluvial soils, on the depressions of the Puttersvlei section.

4. The *Euryops annae - Nemesia fruticans* Semi Woody Shrubland of the high elevation, moist, steep slopes.

5. The *Aristida diffusa - Rhus burchellii* Grassy Shrubland of the doleritic middle plateau.

6. The *Rhigozum obovatum - Garuleum bipinnatum* Dwarf Shrubland on sandstone-mudstone slopes.

7. The *Eriocephalus ericoides - Trichodiadema setuliferum* Dwarf Shrubland of the elevated sandstone pediments and foothills.

8. The *Rhigozum obovatum - Enneapogon desvauxii* Dwarf Shrubland of the rocky dolerite-sandstone foothills.

9. The *Stipagrostis obtusa - Rhigozum obovatum* Dwarf Shrubland of the more arid and denuded rocky sandstone foothills.

10. The *Rhigozum obovatum - Galenia fruticosa* Dwarf Shrubland on the crest of the flat sandstone hills in the Sandrivier section.

11. The *Pentzia incana - Lycium prunus-spinosa* Dwarf Shrubland on the sandstone, mudstone derived foothills and plains.

12. The *Pentzia incana - Monechma incanum* Dwarf Shrubland on the alluvial mudstone gravel deposits.

13. The *Stipagrostis obtusa - Eriocephalus spinescens* Grassy Dwarf Shrubland of the mudstone-sandstone gravel plains.

14. The *Lycium cinereum - Salsola aphylla* Shrubland on Quarternary alluvium.

15. The *Acacia karroo - Stipagrostis namaquensis* Riparian Woodland on deep alluvial soils.

Description of the vegetation

The vegetation changes along a topo-moisture gradient, with a concomitant change in soil type. This distinct geographical and topographical separation of most of the identified plant communities (Figs. 2 & 5) confirms the accuracy of the classification. Along the lower slopes, foothills and plains, soil forms remain predominantly Mispah and Glenrosa with the change in plant communities linked to rockiness and soil depth.

1. The *Eriocephalus ericoides - Pteronia tricephala* Montane Dwarf Shrubland (Fig. 6a).

The *Eriocephalus ericoides - Pteronia tricephala* Montane Dwarf Shrubland occurs on open, flat terrain at moderate elevation (1 620-1 680 m) in the most northern section of the park (Figs. 2 & 5). It is the only Dwarf Shrubland community on the upper plateau within the park. Moving further away from the edge of the mountains, with its associated high rainfall, precipitation declines from 380 mm to around 260 mm (Dent *et al.* 1987). This decline results in a marked aridity gradient that is reflected in the species composition and structure. Karroid dwarf shrubs replace the taller shrubs and grasses.

The habitat of the *Eriocephalus ericoides - Pteronia tricephala* Montane Dwarf Shrubland consists of poorly drained shallow to deeper soils, with a high clay content in the B-horizon. More than 80 % of the area has slopes less than 8 %. The soils are derived from sandstone, siltstone and mudstone illuviation, with the most common soil forms present, the Valsrivier and Oakleaf forms (Land Type Survey Staff 1993). Average canopy cover is 15–25 % with 0–10 % of the soil surface covered by stones. This plant community is small compared to the rest of the upper plateau, and is the only community in the park to occur in land type Db162 (Fig. 2). The high nutrient status of this community attracts most small grazers and browsers occurring in the high elevation areas, with resultant overgrazing and low canopy cover.

The *Eriocephalus ericoides - Pteronia tricephala* Montane Dwarf Shrubland is characterised by Species Group A (Table 1). The

ISSN 0075-6458

Table 1

A phytosociological table of the Karoo National Park.

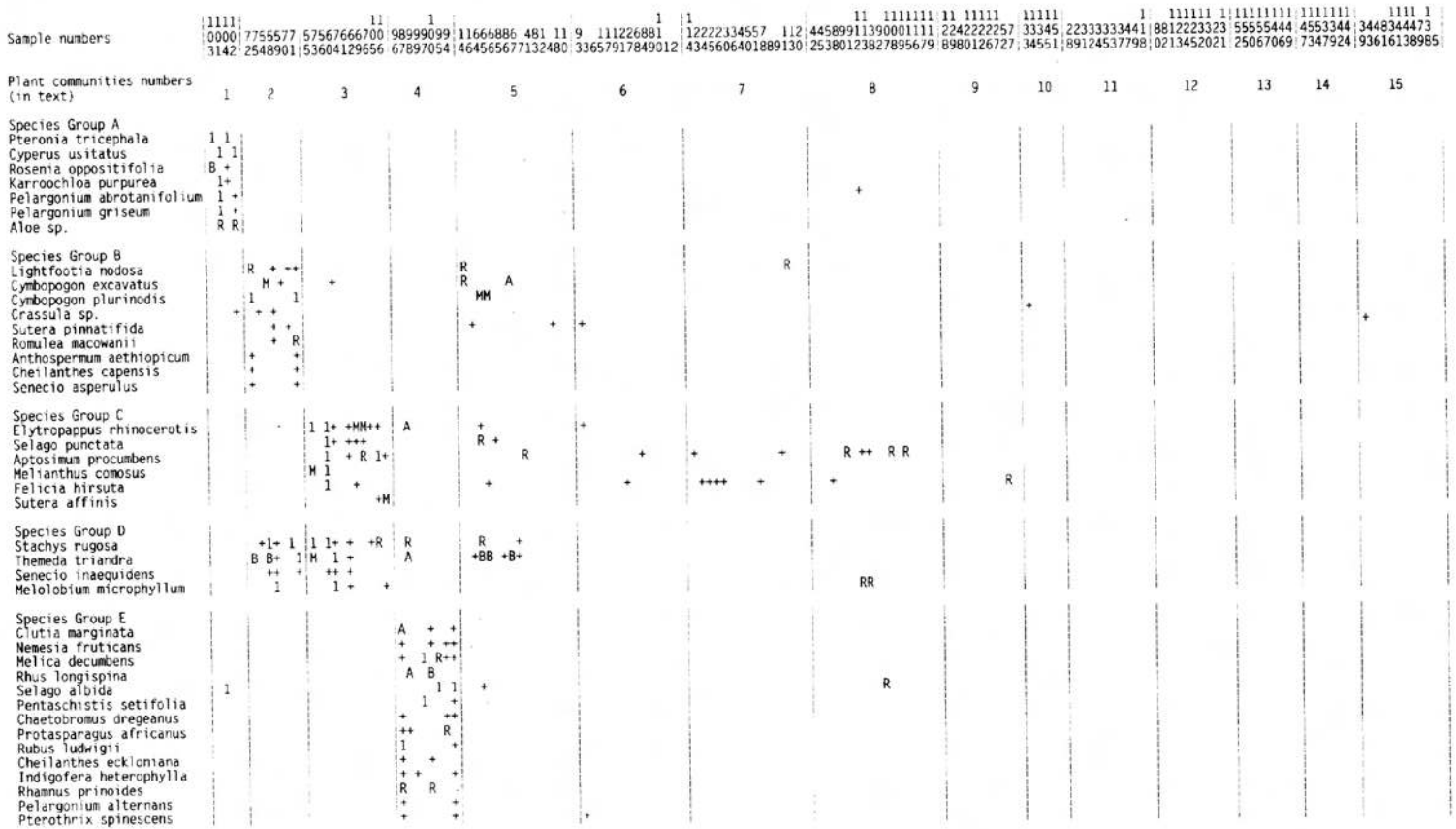
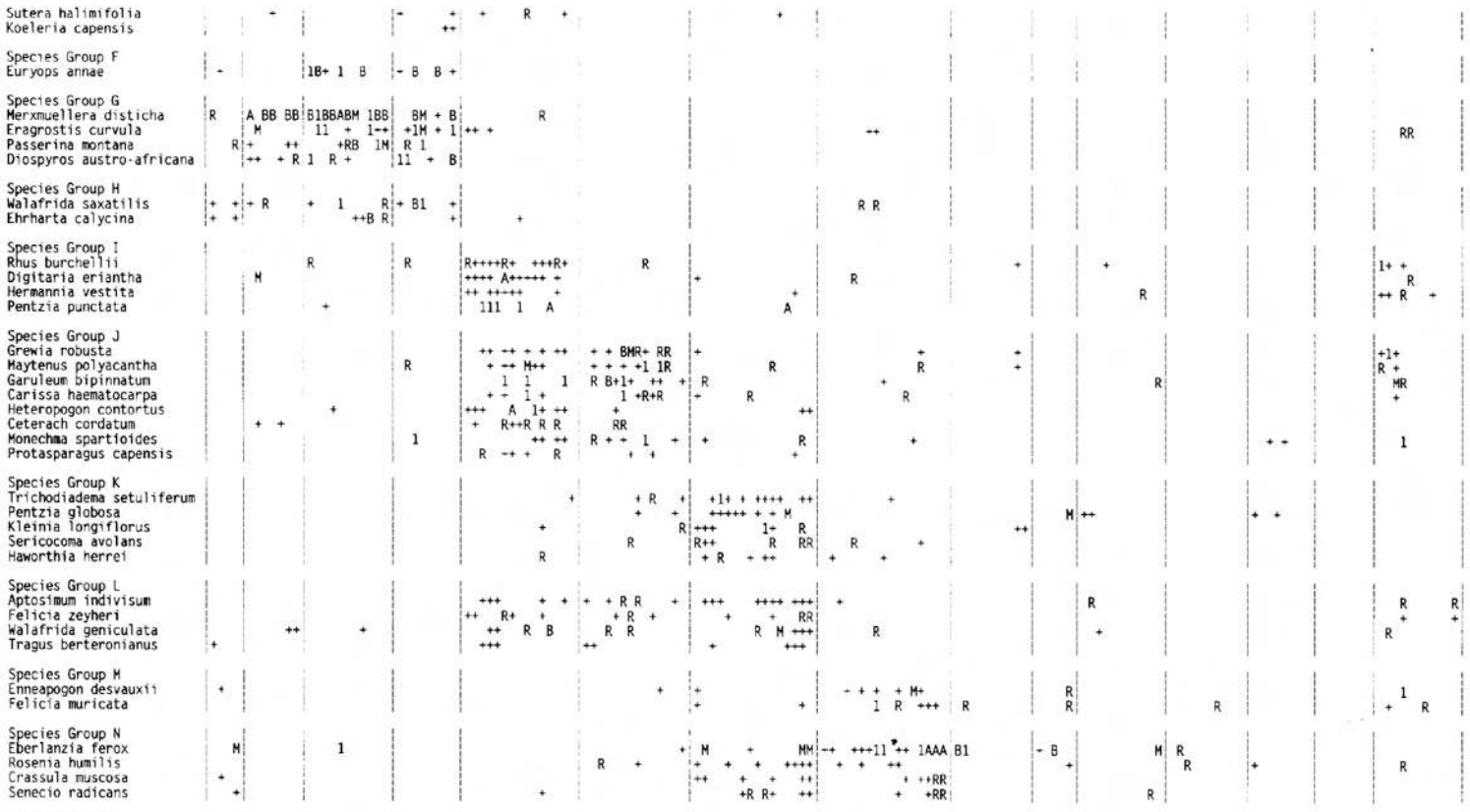
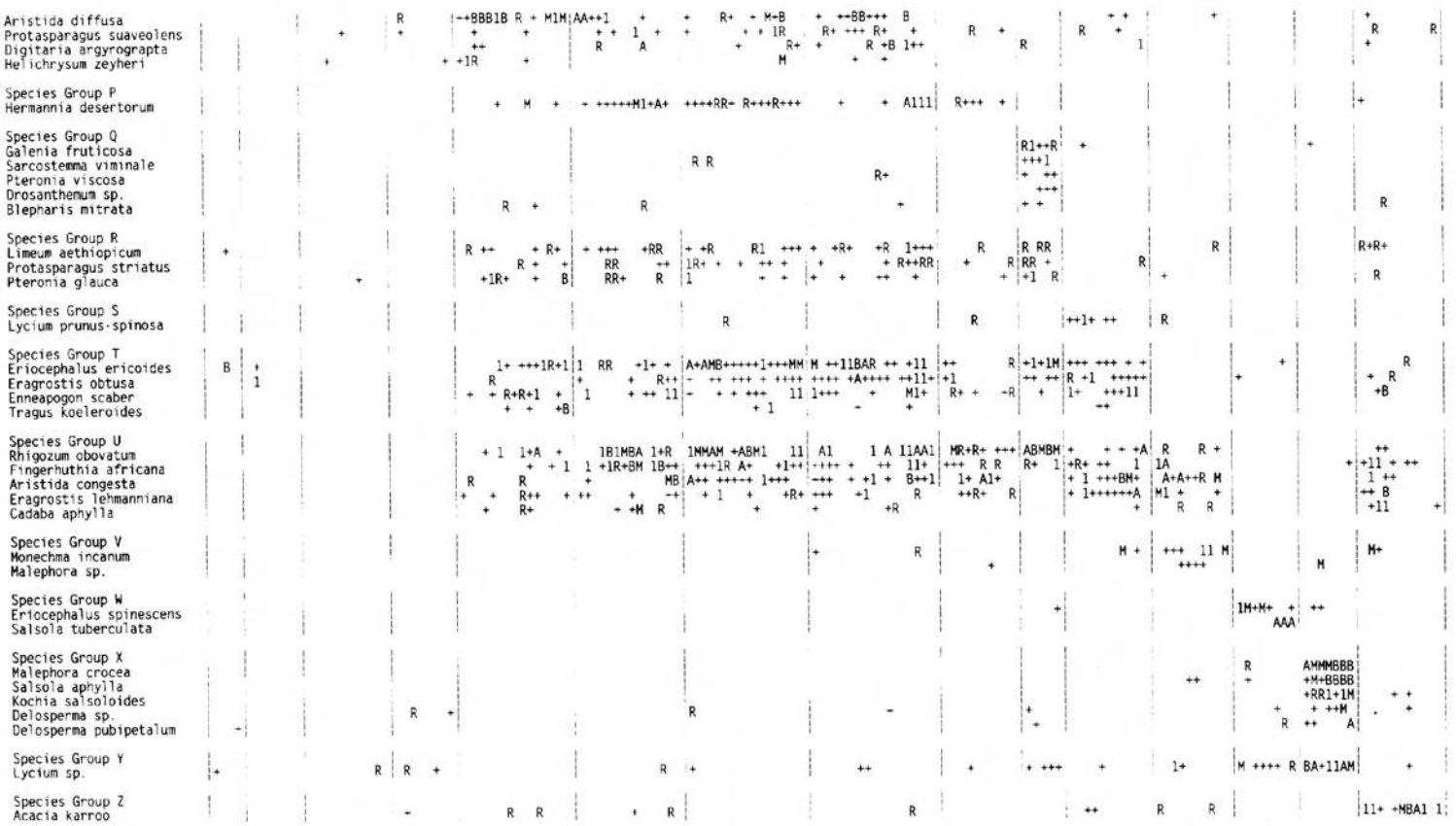


Table 1 (continued)

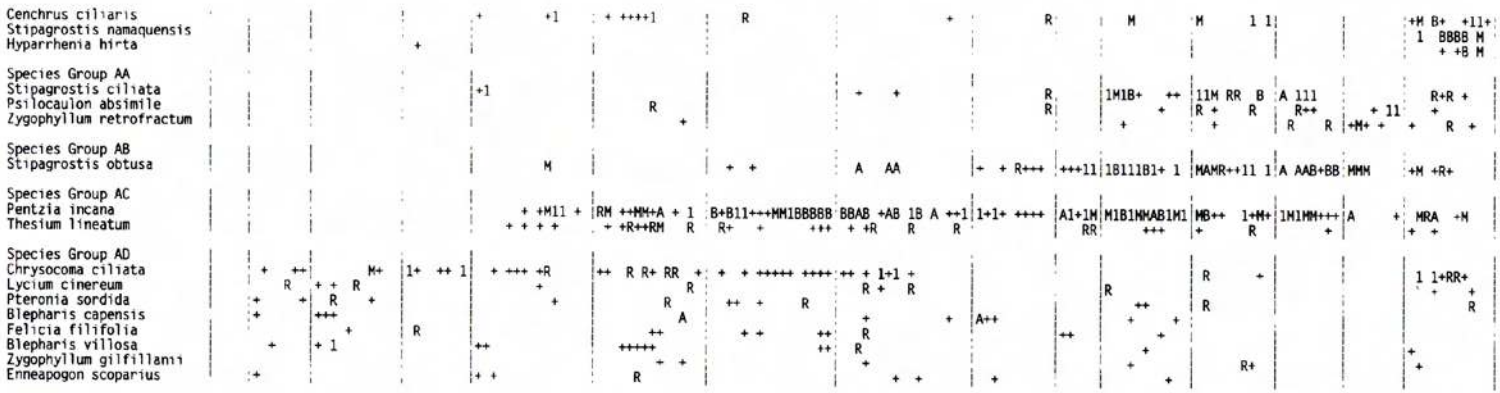


ISSN 0075-6458



ISSN 0075-6458

Table 1 (continued)



ISSN 0075-6458

diagnostic species are the dwarf shrubs, *Pteronia tricephala* and *Rosenia oppositifolia*, and grassy species such as *Karroochloa purpurea* and *Cyperus usitatus*. Species such as *Pelargonium abrotanifolium*, *P. griseum* and *Aloe* sp. are more common in the rocky areas of this community. The grasses *Merxmuellera disticha* (Species Group G) and *Ehrharta calycina* (Species Group H) only occur occasionally while *Walafrida saxatilis* (Species Group H) and *Eriocephalus ericoides* (Species Group T) appear more common. *Walafrida saxatilis* is also an indicator of deteriorating veld condition (Roux *et al.* 1994).

The dwarf shrub layer is generally fairly short (15-20 cm) with *Eriocephalus ericoides* taller up to 30 cm high. Acocks (1988) describes these associated taxa as distinctive of the lower margins of Veld Type 42, (Karroid *Merxmuellera* Mountain Veld replaced by Karoo), and mentions that it could well have been shown as occurring around the margin of nearly all the Karroid *Merxmuellera* Mountain Veld (communities 2 and 3). Acocks (1988) also describes the veld type as virtually the same as the lower southern Karoo, except for the occasional tuft of *Merxmuellera disticha*.

2. The *Merxmuellera disticha - Lightfootia nodosa* Montane Grassland (Fig. 6b).

This Karoo Montane Grassland is situated at high elevation (1 800-1 900 m) (Figs. 2 & 5), with annual rainfall varying from 260-380 mm (Dent *et al.* 1987). Terrain form is variable, with a north-easterly to north-westerly aspect. This community represents a grassland with sparsely scattered shrubs. Historically, fire has been an important component of this ecosystem, with pyrophilic grasses predominating.

Shallow dolerite and sandstone-derived soils of the high rainfall, high elevation regions are associated with this community. The community occurs in landtype Ib256 (Fig. 2), with the dominant soil forms Swartland, with lesser portions of Hutton, Glenrosa and Shortland (Land Type Survey Staff 1993). These soil forms have an abrupt transition in clay content from the A to the B horizon, making the soils prone to erosion. Basal cover is high (45–90 %), with the low cover sites occurring in areas largely covered by rock.

This community is characterised by nine diagnostic species (Species Group B, Table 1), with *Lightfootia nodosa* the most common shrub. The most common grass species in this community are *Merxmuellera disticha* (Species Group G) and *Themeda triandra* (Species Group D). The most conspicuous shrubs are *Passerina montana* and *Diospyros austro-africana* (Species Group G). Flat dolerite outcrops occur in particular in the eastern part of this area, with specialised plant communities containing *Ruschia* spp., *Sarcocaulon* spp., *Euphorbia* spp., *Cotyledon* spp. and *Crassula* species. These specialised communities are not included in the phytosociological survey.

Although this area is mapped as Veld Type 42, (Karroid *Merxmuellera* Mountain Veld replaced by karoo), Acocks (1988) describes these associated taxa as distinctive of Veld Type 60 (Karroid *Merxmuellera* Mountain Veld).

3. The *Euryops annae - Elytropappus rhinocerotis* Montane Shrubland (Fig. 6c).

This community appears as fairly dense perennial shrub patches in localised depressions and shallow valleys in the high altitude *Merxmuellera disticha - Lightfootia nodosa* Montane Grassland (Figs. 2 & 5). The *Euryops annae - Elytropappus rhinocerotis* Montane Shrubland appears to replace *Merxmuellera disticha - Lightfootia nodosa* Montane Grassland where disturbance occurred in the past (Theron *pers. comm.*), while the often more mesic nature of these

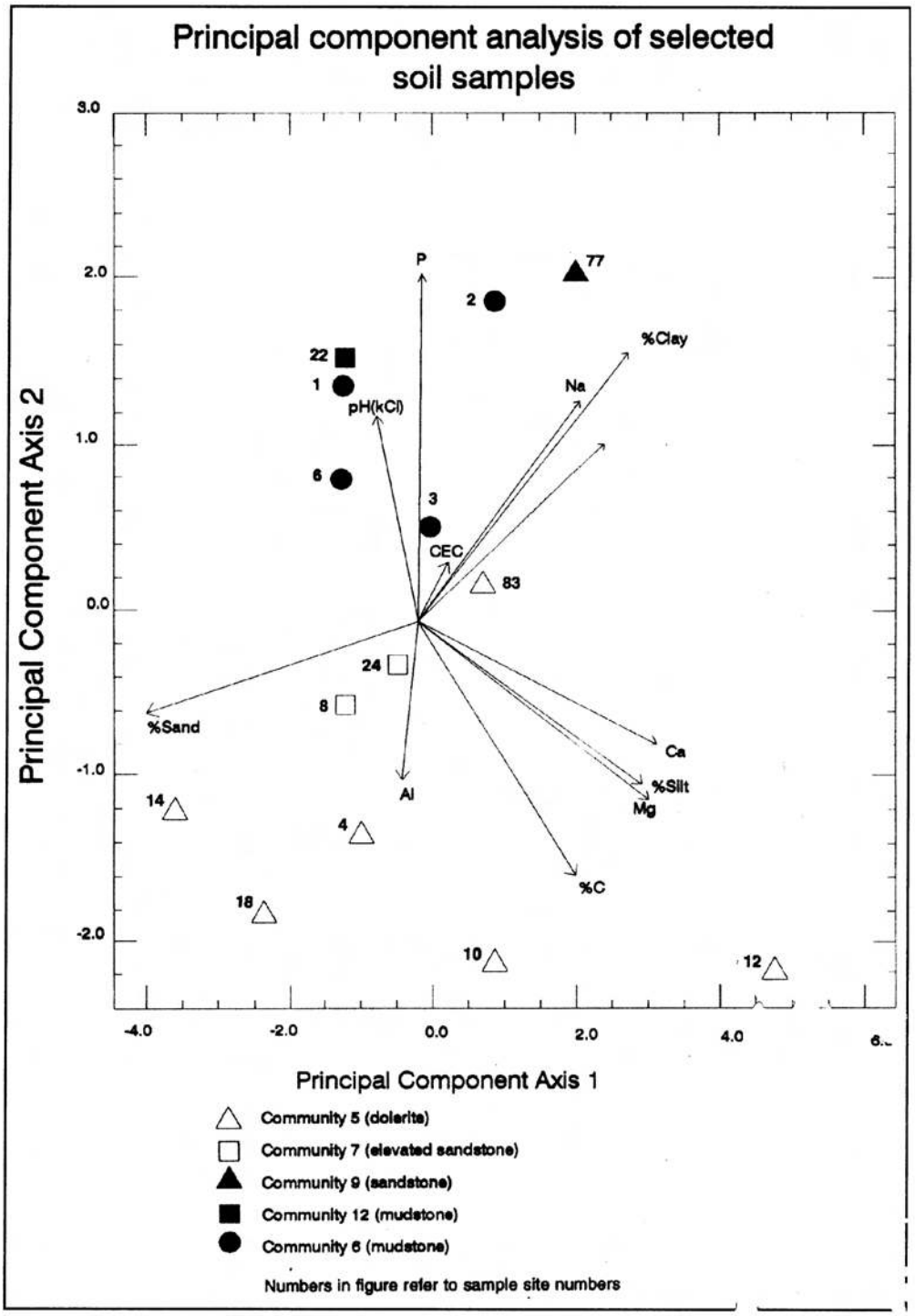


Fig. 4. Bi-plot of the position of soil samples, collected from the middle plateau to the low elevation plains (with communities shown as symbols).

habitats probably also protects them from natural lightning fires that sporadically occur on these mountains. Past cultivation practices are clearly visible in some larger valleys.

The habitat of this community consists of alluvial soils with none to low rockiness and a high canopy cover of 65 - 80 %. Soils are deep with Oakleaf the most common soil form (Land Type Survey Staff 1993). On the outskirts of this community less dense stands of *Elytropappus rhinocerotis*, *Euryops* spp. and *Passerina montana* often occur on the more shallow rocky slopes. None of these species are palatable to grazers (Shearing 1994). Annual forbs that appear after rain remain green longer due to the mesic character of these areas. This attracts many concentrate feeders that occur in this upper region of the park. The land type unit for this community is Ib256 (Fig. 2).

The *Euryops annae - Elytropappus rhinocerotis* Montane Shrubland is characterised by the absence of Species Groups B and E, and by the presence of diagnostic shrub species *Elytropappus rhinocerotis*, and the dwarf-shrubs and forbs *Selago punctata*, *Aptosimum procumbens*, *Melianthus comosus*, *Felicia hirsuta* and *Sutera affinis* (Species Group C, Table 1). Other dominant species that occur in these communities are the shrub *Euryops annae* and the grass *Merxmuellera disticha*.

4. The *Euryops annae - Nemesia fruticans* Semi Woody Shrubland

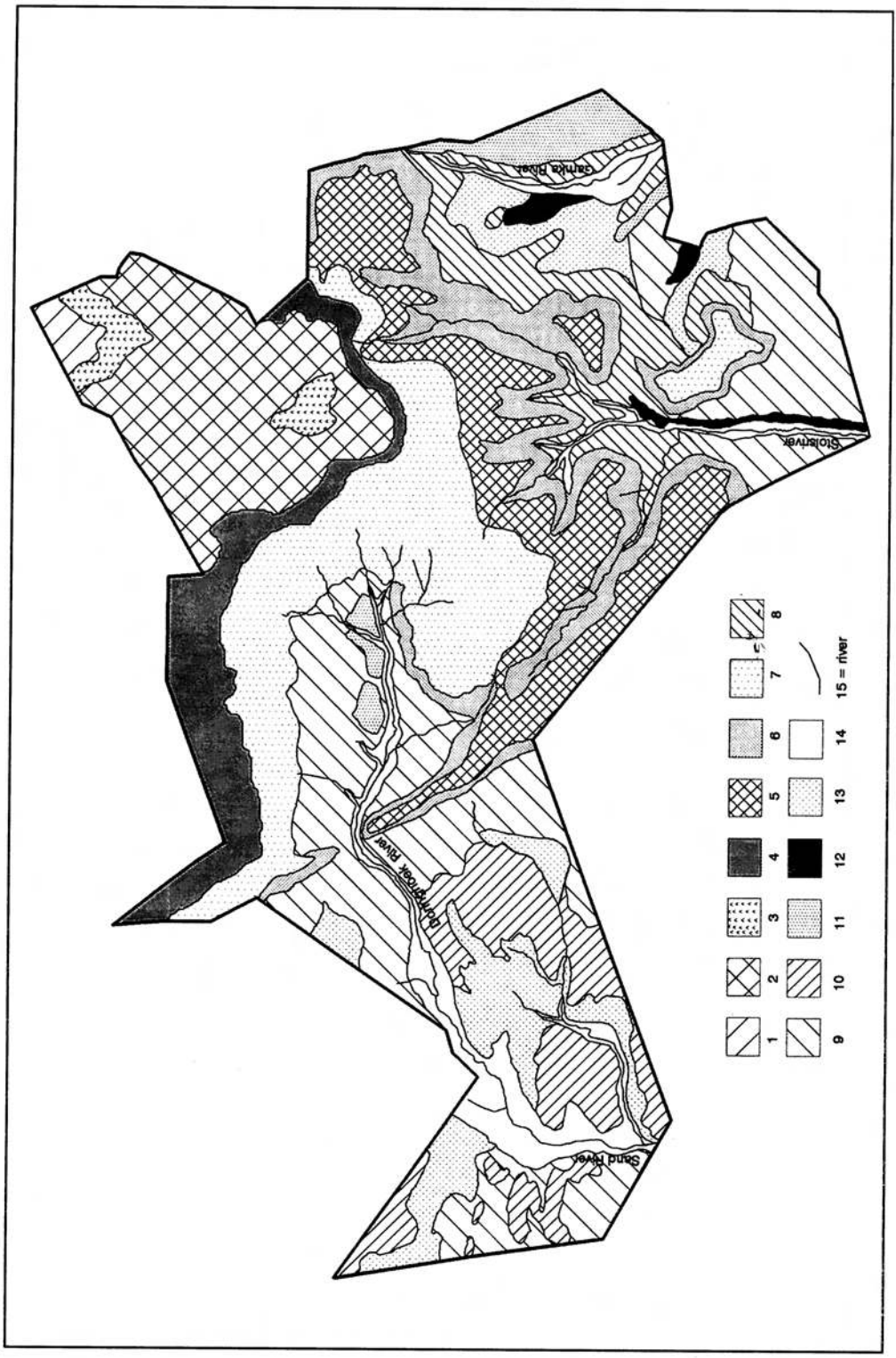
This community occurs on the steep south-westerly and southeasterly slopes directly below the escarpment (Figs. 2 & 5) which consists of rocky sandstone screes interspersed with less rocky areas, and drier areas interspersed with wetter areas where the sun is absent in winter and in the afternoons. The *Euryops annae - Nemesia fruticans* Semi Woody Shrubland generally has a high canopy cover (60–75 %) and high species diversity.

The *Euryops annae - Nemesia fruticans* Semi Woody Shrubland is characterised by 16 diagnostic species (Species Group E, Table 1) with the shrubs *Rhus longispina*, *Rubus ludwigii* and *Rhamnus prinoides* occasionally occurring in high densities. Other common species include the shrubs *Euryops annae* (Species Group F) in high densities, *Passerina montana* and *Diospyros austro-africana* (Species Group G), the dwarf shrub *Walafrida saxatilis* (Species Group H), and the grasses *Merxmuellera disticha* and *Eragrostis curvula* (Species Group G). Lower down the steep slopes *Elytropappus rhinocerotis* becomes more prevalent.

5. The *Aristida diffusa - Rhus burchellii* Grassy Shrubland (Fig. 6d).

This community is situated on the flat middle escarpment, at an elevation that varies from 920-1250 m (Figs. 2 & 5). The high shrub and grass component of this community suggests a mesic site, probably due to the precipitation deposited by the south westerly fronts that predominate in the region. Median annual rainfall varies from 202 mm to 352 mm (Dent *et al.* 1987). Soils are a shallow (<1,0 m) Mispah rock complex (Land Type Survey Staff 1993). Chemical analysis of the soil revealed elevated Al, Mg and organic carbon. The *Aristida diffusa - Rhus burchellii* Grassy Shrubland is typical of land type Ib257 (Fig. 2). Basal cover and rockiness complement one another, with one or the other being high.

The diagnostic species (Species Group I, Table 1) are *Rhus burchellii*, *Digitaria eriantha*, *Hermannia vestita* and *Pentzia punctata*. Shrub clumps occur at regular intervals, with intertwined shrubs such as *Grewia robusta*, *Maytenus polyacantha*, *Carissa haematocarpa* (Species Group J), *Lycium* spp., *Rhus burchellii*, and occasionally *Acacia karroo*. Many of these shrub species also occur down the slopes towards the


Sarmie River
Olifantsrivier
Buffelsdoorn River
Sand River
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15 = river

lower plains (community 6). The dominant grass is *Aristida diffusa*, although *Themeda triandra*, *Cymbopogon excavatus* and *C. plurinodis* also occur in high densities in localised areas. Other species that are common are the dwarf shrubs *Eriocephalus ericoides*, *Rhigozum obovatum*, *Pentzia incana* and *Chrysocoma ciliata*, the grasses *Heteropogon contortus* and to a lesser extent *Eragrostis lehmanniana* and *Enneapogon scabra*. This community is related to the Grassy Mountain Scrub (Veld Type 26c) section of the Karroid Broken Veld of Acocks (1988). Acocks (1988) accurately describes this community as invaded to varying degrees by Karoo and Renosterveld (*Elytropappus rhinocerotis*).

6. The *Rhigozum obovatum - Garuleum bipinnatum* Dwarf Shrubland (Fig. 6e).

The *Rhigozum obovatum - Garuleum bipinnatum* Dwarf Shrubland occurs on steep, unstable to stable mudstone/sandstone slopes, with the occasional influence of dolerite (Figs. 2 & 5). The Mispah and Glenrosa soil forms have 75 % rockiness. Exposure of these soils leads to serious gully erosion. The prominent lower mountain slopes of Land type Ib255, and the more arid unstable mudstone slopes of land type Fc184 (Land Type Survey Staff 1993) in the Sandrivier area, are characteristic of this community. Elevation is low to moderate (890 - 1 080 m) with a low to moderate rainfall (150-260 mm) (Dent *et al.* 1987).

Vegetation cover varied markedly with lower cover values on the warmer sandstone-mudstone slopes (13-25 %), compared to the cooler less exposed slopes with doleritic influence (35 %).

This community is characterised by the absence of any diagnostic species, the presence of Species Group J, with shrubs such as *Grewia robusta*, *Maytenus polyacantha* and *Carissa haematocarpa*, and the absence of Species Group I. Species commonly found against these slopes are the dwarfshrubs *Garuleum bipinnatum* and *Monechma spartioides* (Species Group J, Table 1) while the shrub *Cadaba aphylla* (Species Group U), the dwarf shrubs *Hermannia desertorum* (Species Group P), *Limeum aethiopicum* (Species Group R), *Rhigozum obovatum* (Species Group U), *Pentzia incana* and *Thesium lineatum* (Species Group AC) and the grass species *Fingerhuthia africana* (Species Group U) also occur in high densities.

Fig. 5. A vegetation map of the dominant plant communities in the Karoo National Park. (1) The *Eriocephalus ericoides - Pteronia tricephala* Montane Dwarf Shrubland, (2) The *Merxmuellera disticha - Lightfootia nodosa* Montane Grassland, (3) The *Euryops annae - Elytropappus rhinocerotis* Montane Shrubland, (4) The *Euryops annae - Nemesia fruticans* Semi Woody Shrubland, (5) The *Aristida diffusa - Rhus burchellii* Grassy Shrubland, (6) The *Rhigozum obovatum - Garuleum bipinnatum* Dwarf Shrubland, (7) The *Eriocephalus ericoides - Trichodiadema setuliferum* Dwarf Shrubland, (8) The *Rhigozum obovatum - Enneapogon desvauxii* Dwarf Shrubland, (9) The *Stipagrostis obtusa - Rhigozum obovatum* Dwarf Shrubland, (10) The *Rhigozum obovatum - Galenia fruticosa* Dwarf Shrubland, (11) The *Pentzia incana - Lycium prunus-spinosa* Dwarf Shrubland, (12) The *Pentzia incana - Monechma incanum* Dwarf Shrubland, (13) The *Stipagrostis obtusa - Eriocephalus spinescens* Grassy Dwarf Shrubland, (14) The *Lycium cinereum - Salsola aphylla* Shrubland, and (15) The *Acacia karroo - Stipagrostis namaquensis* Riparian Woodland.

7. The *Eriocephalus ericoides - Trichodiadema setuliferum* Dwarf Shrubland (Fig. 6f).

The *Eriocephalus ericoides - Trichodiadema setuliferum* Dwarf Shrubland typically occurs in repetitive patterns on the flat sandstone pediments present in varying degrees on the mountain slopes and foothills (Figs. 2 & 5). Elevation varies from approximately 1 100 to <900 m. Geology is generally sandstone and vegetation cover varies between 20 and 50 %. These plant communities occur on the crests (4 %) of Land type Ib255, with 50 % rock, 30 % Mispah and 20 % Glenrosa soil forms (Land Type Survey Staff 1993). This community occurs in less arid sites (200-250 mm, Dent *et al.* 1987).

The *Eriocephalus ericoides - Trichodiadema setuliferum* Dwarf Shrubland is characterised by the diagnostic species *Trichodiadema setuliferum*, *Pentzia globosa*, *Kleinia longiflorus*, *Sericocoma avolans* and *Haworthia herrei* (Species Group K, Table 1). Dwarf shrubs are dominant in this community with species such as *Aptosimum indivisum*, *Hermannia desertorum*, *Limeum aethiopicum*, *Eriocephalus ericoides*, *Rhigozum obovatum* and *Pentzia incana*. Grasses that frequently occur in this community, but less abundant, are *Eragrostis obtusa*, *Enneapogon scaber*, *Fingerhuthia africana*, and to a lesser extent *Digitaria argyrograpta*, which generally occur where grazing is in a good condition.

8. The *Rhigozum obovatum - Enneapogon desvauxii* Dwarf Shrubland (Fig. 6g).

The *Rhigozum obovatum - Enneapogon desvauxii* Dwarf Shrubland occurs on the foothills (900–960 m), typically found around the main camp site, around Stolshoek and on the first section of the circular drive of Lammertjiesleegte (Fig.5). Veld condition is generally good in these areas as opposed to the often adjacent communities (9 & 11).

The habitat of this Dwarf Shrubland consists of stony sandstone apron veld and foothills, with round dolerite rocks strewn across the surface. The soils are predominantly of the Glenrosa and Mispah forms. Vegetation occurring on low elevation dolerite dykes also fall into this plant community. The slope is gradual (2 - 10 %) and most of the survey sites have an easterly aspect and occur in Land type Fc385 (Fig. 2). Rock cover varies between 30 and 60 % and vegetation cover between 5 and 40 %.

Species Group M (Table 1) characterises this community, which includes the diagnostic dwarf shrub *Felicia muricata* and the grass *Enneapogon desvauxii*. Species diversity is high in the less overgrazed areas, with the succulent dwarf shrub *Eberlanzia ferox* (Species Group N) more abundant in the less grassy areas. Common species that occur in high densities are the dwarf shrubs *Hermannia desertorum* (Species Group P), *Limeum aethiopicum* (Species Group R), *Eriocephalus ericoides* (Species Group T), *Rhigozum obovatum* (Species Group U) and *Pentzia incana* (Species Group AC). Prominent grass species in localised areas in this community are *Aristida diffusa*, *Digitaria argyrograpta* (which suggests less arid conditions, Species Group O) and *Stipagrostis obtusa* (Species Group AB). Other common species are *Rosenia humilis*, *Crassula muscosa*, *Senecio radicans* (Species Group N), *Protasparagus suaveolens* (Species Group O), *Protasparagus striatus*, *Pteronia glauca* (Species Group R), *Thesium lineatum* (Species Group AC), and grass species such as *Eragrostis obtusa*, *Enneapogon scaber*, *Tragus koeleroides* (Species Group T), *Fingerhuthia africana*, *Aristida congesta*, and *Eragrostis lehmanniana* (Species Group U).

9. The *Stipagrostis obtusa - Rhigozum obovatum* Dwarf Shrubland (Fig. 6h).

This community occurs in the lower more arid and denuded rocky footslopes and plains

Fig. 6. Examples of the major plant communities (a-n) of the Karoo National Park.



a. The *Eriocephalus ericoides - Pteronia tricephala* Montane Dwarf Shrubland

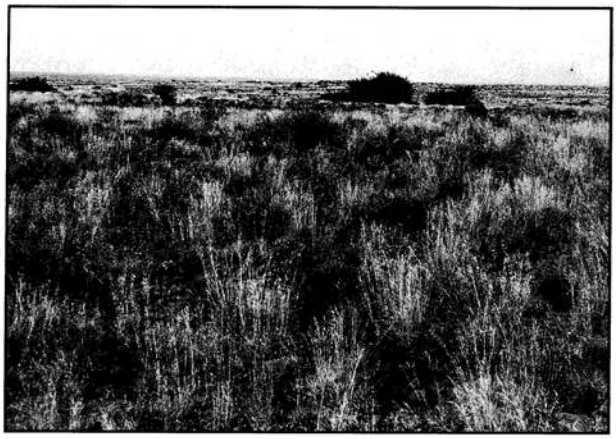


b. The *Merxmuellera disticha - Lightfootia nodosa* Montane Grassland



c. The *Euryops annae - Elytropappus rhinocerotis* Montane Shrubland

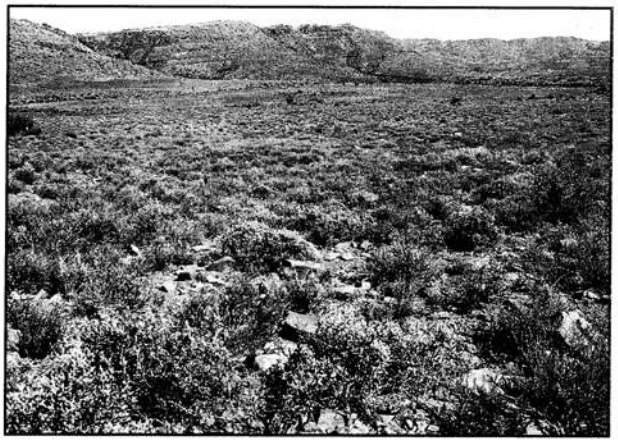
of Lammertjiesleegte, Sandrivier and Doornhoek in Land type Fc184 and Fc385 (Land Type Survey Staff 1993) (Figs. 2 & 5). The soils are also predominantly of the Glenrosa and Mispah forms. The sandstone has none to little dolerite rocks strewn on top. Veld condition appears generally poorer than in the previous communities. Slope is virtually flat, rock cover is on average 24 % and the average vegetation canopy cover is 16 %. The *Stipagrostis obtusa - Rhigozum obovatum* Dwarf Shrubland is characterised by the absence of Species Group O and the presence of Species Group P and of the grass *Stipagrostis obtusa* (Species Group AB) (Table 1). Common species in this community are *Hermannia desertorum* (Species Group P), *Rhigozum obovatum* (Species Group U), *Pentzia incana* (Species Group AC), and the grasses *Enneapogon scaber* (Species Group T), *Fingerhuthia africana*, *Aristida congesta* and *Eragrostis lehmanniana* (Species Group U). Patches of elevated nutrients attract herbivores to this community, causing degradation in localised areas.



d. The *Aristida diffusa - Rhus burchellii* Grassy Shrubland



e. The *Rhigozum obovatum - Garuleum bipinnatum* Dwarf Shrubland



f. The *Eriocephalus ericoides - Trichodiadema setuliferum* Dwarf Shrubland

10. The *Rhigozum obovatum - Galenia fruticosa* Dwarf Shrubland (Fig. 6i).

This community occurs on the flat crests of sandstone hills in Land type Fc184 (Land Type Survey Staff 1993) in the Sandrivier area of the park (Figs. 2 & 5). Elevation is low (800-900 m), rock cover is generally very high (>60 %), and soils are predominantly of the Mispah form, with smaller portions of Glenrosa. Vegetation canopy cover is generally fairly low (20 %) due to the rockiness of the terrain. Rockiness is high on the edge of the hills, with an accumulation of silt towards the convex centres.

Species Group Q (Table 1) characterises the *Rhigozum obovatum - Galenia fruticosa* Dwarf Shrubland, with diagnostic dwarf shrubs *Galenia fruticosa*, *Pteronia viscosa* and *Blepharis mitrata*, and the more succulent *Sarcostemma viminale* and *Drosanthemum* sp. The most dominant species in this community is *Rhigozum obovatum* (Species Group U). Other common species are the dwarf shrubs *Limeum aethiopicum*, *Protasparagus striatus*, *Pteronia glauca* (Species Group R), *Eriocephalus ericoides* (Species Group T), *Pentzia incana*, *Thesium lineatum* (Species Group AC) and *Chrysocoma ciliata* (Species Group AD). Common but sparse grasses are *Eragrostis obtusa* (Species Group T), *Fingerhuthia africana* (Species

Group U) and *Stipagrostis obtusa* (Species Group AB).

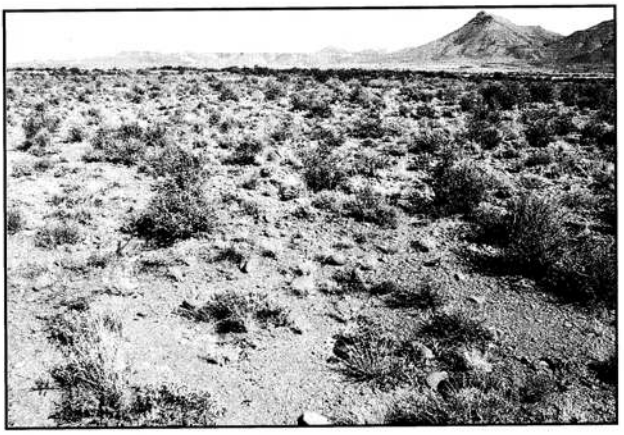
11. The *Pentzia incana - Lycium prunus-spinosa* Dwarf Shrubland (Fig. 6j).

The *Pentzia incana - Lycium prunus-spinosa* Dwarf Shrubland occurs on the sandstone plains and footslopes of Land types Ib255, Fc184 and Fc385 (Land Type Survey Staff 1993) (Figs. 2 & 5). Annual rainfall is 180-250 mm (Dent *et al.* 1987). Species diversity is low and annual plants attract many springbok after rainfall events. Vegetation cover varies between 20 and 45 %, and rock cover is generally very low, consisting of sandstone stones with varying quantities of mudstone gravel.

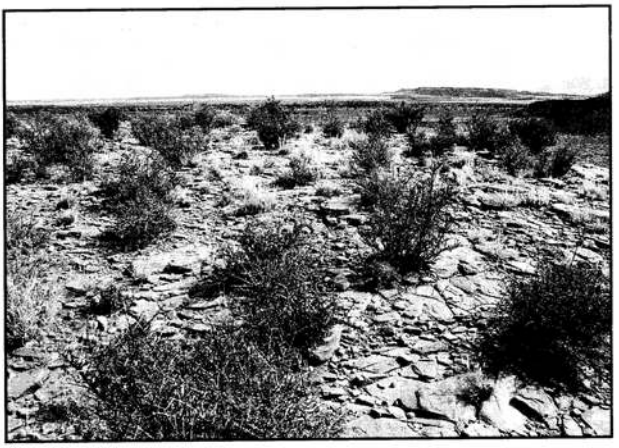
This community is characterised by the diagnostic species *Lycium prunus-spinosa* (Species Group S, Table 1), and the dominance of the dwarf shrub *Pentzia incana* (Species Group AC). Grass species common in the lower lying plains are *Aristida congesta* (Species Group U), *Stipagrostis ciliata* (in localised areas) (Species Group AA) and *Stipagrostis obtusa* (Species Group AB). Other common but sparse grass species that occur in this community are *Eragrostis obtusa*, *Enneapogon scaber* (Species Group T), and *Eragrostis lehmanniana* (Species Group U). The shrub *Rhigozum obovatum* is gener-



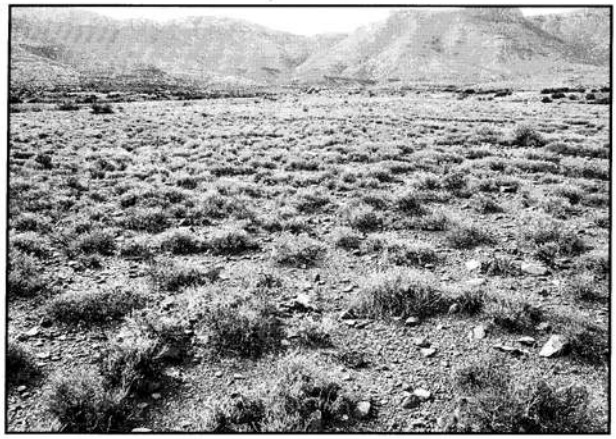
g. The *Rhigozum obovatum - Enneapogon desvauxii* Dwarf Shrubland



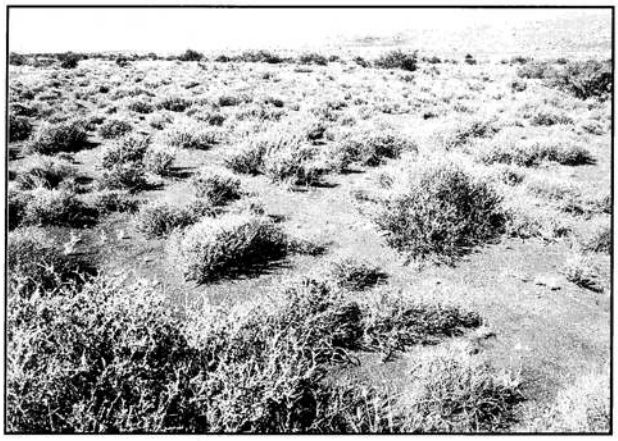
h. The *Stipagrostis obtusa - Rhigozum obovatum* Dwarf Shrubland



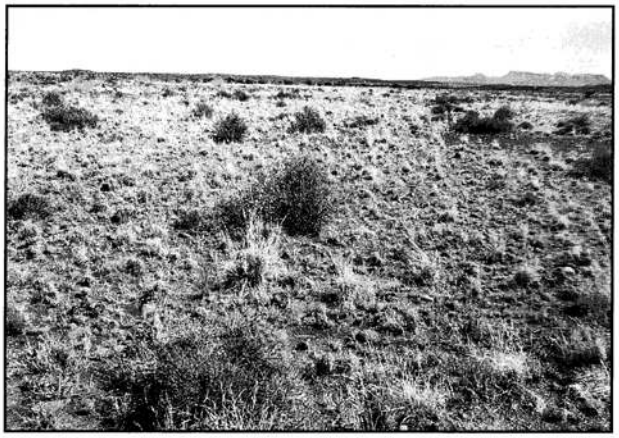
i. The *Rhigozum obovatum - Galenia fruticosa* Dwarf Shrubland



j. The *Pentzia incana - Lycium prunus-spinosa* Dwarf Shrubland



k. The *Pentzia incana - Monechma incanum* Dwarf Shrubland



l. The *Stipagrostis obtusa - Eriocephalus spinescens* Grassy Dwarf Shrubland

ally conspicuous in its absence in this community, while it usually occurs in the adjacent more rocky areas (communities 8 & 9).

12. The *Pentzia incana - Monechma incanum* Dwarf Shrubland (Fig. 6k).

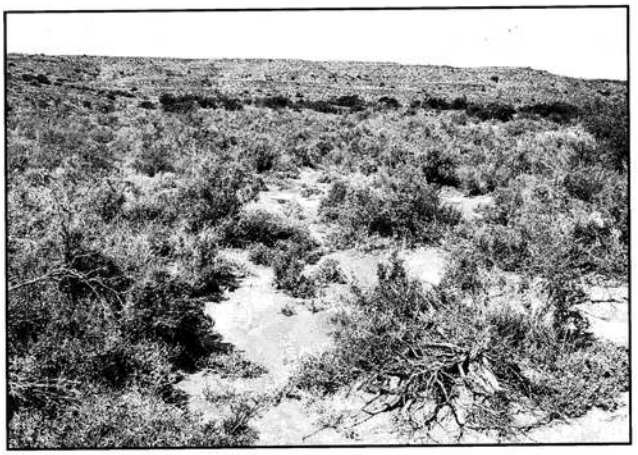
The *Pentzia incana - Monechma incanum* Dwarf Shrubland always occurs adjacent to community 11, in low-lying areas where drainage lines or rivers deposit alluvial mudstone gravel (Figs. 2 & 5). Aspects and slopes are flat, with the vegetation cover varying between 5 % and 25 %. The soil of this community consist of deep fine to coarse gravel. Good examples of this community occur in Land type Fc385 (Land Type Survey Staff 1993) in the Lammertjiesleegte section of the park.

The *Pentzia incana - Monechma incanum* Dwarf Shrubland is characterised by the diagnostic dwarfshrub species *Monechma incanum* and the succulent *Malephora* sp. (Species Group V, Table 1). Common species are *Aristida congesta* (Species Group U), *Stipagrostis ciliata* (Species Group AA), *S. obtusa* (Species Group AB), and *Pentzia incana* (Species Group AC). *Psilocaulon absimile* and *Monechma incanum* occurs in pure stands in localised areas. *Acacia karroo*

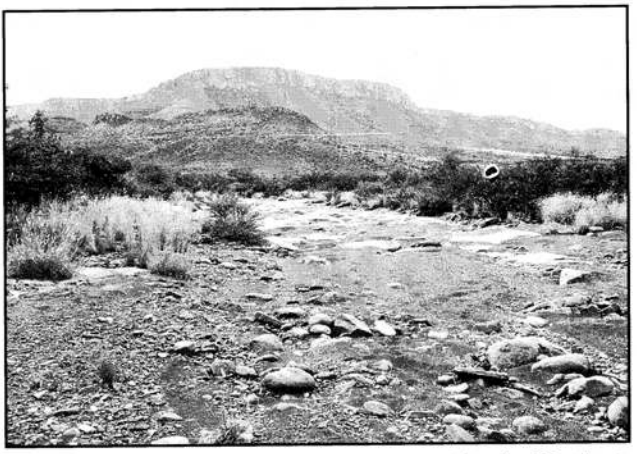
and *Cenchrus ciliaris* is present along the narrow drainage lines that cross these communities.

13. The *Stipagrostis obtusa* - *Eriocephalus spinescens* Grassy Dwarf Shrubland (Fig. 6l).

This community occurs at low elevations (800 - 900 m) and low rainfall (160-170 mm) (Dent *et al.* 1987), on the almost flat footslopes and plains in the Sandrivier and Lammertjiesleegte section of the park (Figs. 2 & 5). The community is predominantly grassy, and generally occurs adjacent the *Lycium cinereum* - *Salsola aphylla* Shrubland (community 14) in Land types Fc385, 184 and 181 (Land Type Survey Staff 1993). The lithology is mudstone and sandstone gravel with localised areas where surface lime is present, with Mispah the most common soil form (Land Type Survey Staff 1993). Stoniness (5 %) and vegetation cover (10-25 %) is generally very sparse.



m. The *Lycium cinereum* - *Salsola aphylla* Shrubland



n. The *Acacia karroo* - *Stipagrostis namaquensis* Riparian Woodland

Species Group W (Table 1) characterises the *Stipagrostis obtusa* - *Eriocephalus spinescens* Grassy Dwarf Shrubland, with the diagnostic dwarfshrub species *Eriocephalus spinescens*, and in localised areas where surface lime is present, *Salsola tuberculata*. Other species that occur in high densities are *Stipagrostis ciliata* (Species Group AA), *S. obtusa* (Species Group AB), *Pentzia incana* (Species Group AC) and *Lycium cinereum* (Species Group Y), which is also common in the adjacent *Lycium cinereum* - *Salsola aphylla* Shrubland. Gemsbok (*Oryx gazella*) particularly favoured *Stipagrostis ciliata* during the study period.

Vorster & Roux (1983) described this veld as generally degraded. They mentioned that *Salsola tuberculata* - *Stipagrostis obtusa* veld in the north western Karoo (veld in good condition) may result in a copper deficiency in stock. This may cause sway-back disease, bone fractures and anaemia in lambs.

14. The *Lycium cinereum - Salsola aphylla* Shrubland (Fig. 6m).

The *Lycium cinereum - Salsola aphylla* Shrubland is situated in flat, low elevation floodplain areas (Figs. 2 & 5). Good examples are visible in Lammertjiesleegte next to the Gamka River and in Sandrivier and Doornhoek next to the Sand and Doornhoek Rivers (Fig. 5). Soils consist of silt and sediment deposits, and are calcareous with a fine powdery texture. These soils are duplex soils and fall into Land types Fc181, 184 and 385 (Land Type Survey Staff 1993)(Fig. 2). Leaching of salts and the salinisation of the soils is an integral part of the erosion process in these areas (Roux & Opperman 1986). Symptoms of erosion are conspicuous in localised areas, with brackish bare patches or deep gullies visible in some floodplains of Sandrivier. Although the general environment is extremely arid, with low rainfall (160-180 mm) and high evaporation, well-conserved communities thrive on the stored moisture of the deep silty soils. Because of the poorly drained nature of these floodplains, salinisation produces salt tolerant vegetation such as *Kochia* spp., *Salsola* spp., and *Zygophyllum* species (Roux & Opperman 1986).

Species Group X (Table 1) characterises the *Lycium cinereum - Salsola aphylla* Shrubland. The diagnostic plants are the shrubs *Salsola aphylla* and *Kochia salsoloides*, and succulents *Malephora crocea*, *Delosperma* sp. and *Delosperma pubipetalum*. *Lycium cinereum* also occurs in high densities, and to a lesser extent *Psilocaulon absimile*, *Zygophyllum retrofractum* (Species Group AA), *Stipagrostis obtusa* (Species Group AB), and *Pentzia incana* (Species Group AC). This community contains examples of past overgrazing, with a browse line visible in some almost pure *Salsola aphylla* stands, where the shrub layer can be 1.5–2.0 m tall. Canopy cover varies between 15 % and 45 %, while rocks and stones are virtually absent. *Lycium cinereum* dominates the general shrub layer (0.6 m) which is on average taller than the surrounding dwarf shrub communities.

Burrowing animals and animals using old burrows favour the *Lycium cinereum - Salsola aphylla* Shrubland, e.g. aardvark (*Orycteropus afer*), bat-eared foxes (*Otocyon megalotis*) and porcupine (*Hystrix africaeaustralis*). The cultivation and subsequent destruction of these communities along rivers have also led to the threatened status of the riverine rabbit (*Bunolagus monticularis*) (Duthie 1989).

15. The *Acacia karroo - Stipagrostis namaquensis* Riparian Woodland (Fig. 6n).

Distinctive woody communities are found along the drainage lines of all Karoo landscapes (Fig. 5). These communities are often the only densely vegetated areas, and provide refuge and palatable browse for black rhinoceros (*Diceros bicornis*), kudu (*Tragelaphus strepsiceros*) and eland (*Taurotragus oryx*). In the flat lowlying areas of the Sand River, the river bed broadens and provides a savanna landscape with a dense grass cover.

Species Group Z (Table 1) characterises the *Acacia karroo - Stipagrostis namaquensis* Riparian Woodland. This is an area of maximum disturbance, with unpredictable flooding making it an extremely unstable habitat. Taxa from many different communities are encountered (Species Groups I, J, T & U), with the woody species being most successful and obvious. *Acacia karroo* dominates in this community, but other species may include *Grewia robusta*, *Maytenus polyacantha* (Species Group J), *Diospyros lycioides* and *Rhus lancea*. *Cynodon incompletus* often dominates the grass species, with perennial taxa such as *Cenchrus ciliaris*, *Stipagrostis namaquensis* and *Hyparrhenia hirta* (Species Group Z) occurring in scattered, well established clumps. Cover varies both spatially and temporally, as moisture levels fluctuate. The deep, sandy alluvium provides an ideal

germination environment for many annual taxa, e.g. *Atriplex lindleyi* subsp. *inflata*, *Delosperma* sp. and *Atriplex* species. This community dissects patterns in the landscape and does not parallel the topomoisture gradients of the region.

16. Specialised communities.

In this document no specialised communities are described. Examples that may deserve further attention include:

i) High elevation wetlands
This is a specialised community of the high elevation drainage lines. Associated species observed include *Tetrachne dregei* and *Helictotrichon* sp. Some burning of this community should be undertaken to encourage these species. *Arundo donax* is an introduced alien that should be systematically removed.

ii) High elevation flat rocky outcrops with succulents.

iii) Cliff communities.

iv) Narrow dolerite dykes.

Plant-soil Relationships

Following the detailed analysis of fourteen soil samples collected from the middle plateau to the low elevation plains, the variable values were investigated using principle components analysis (Statgraphics 1989). The first two principle component axes accounted for 55 % of the variation in the data. Using these two component axes, a biplot (Fig. 4) was produced, displaying the position of the various communities in relation to the major soil variables. In the biplot, the arrows directed away from the origin show the direction of increase in soil variables. The first principle component axis, which accounts for 35 % of the variation, is dominated by changes in soil texture, Ca and Mg. The second principle component axis, which accounts for 20 % of the variation, is dominated by changes in total P and pH (KCl). Samples from the lowlying communities (sample site numbers 1, 2, 3, 6, 22 and 77 (Table 1)) are distinguishable from the middle plateau communities by having higher pH values (more alkaline), Phosphate, Na, K and clay fractions. With the middle plateau soils, there is a sand-silt gradient separating out the samples. The same differentiating features of the soils have been found in the Karoo Nature Reserve (Palmer 1991b), and the similarity between the two results is an important confirmation of the soil chemical patterns in the region. The high nutrient status soils of the pediments are important. Although precipitation may be limited, nutrients are plentiful and rainfall events provide the stimulus for elevated production.

Concluding remarks

Fifteen mappable plant communities were recognised and described. This is one of the first approximations of the communities of the Great Karoo following the efforts of Acocks (1988) and Vorster (1985b). Floristic patterns in the landscape, associated with coarse environmental variables (elevation, rainfall, substrate, land type) have been identified. It has not been possible within the constraints of the project to build causal relationships between communities and their environments. However, landscape patterns have been elucidated, which suggest a complex heterogeneous flora. The vegetation has been described using traditional methods. The results suggest that the Karoo National Park contain healthy representative examples of Nama-Karoo communities.

The environmental gradient that contributes the most to biotic diversity in the system is the topo-moisture gradient, extending from

JOHNSON, M.R. & A.W. KEYSER. 1979. *The geology of the Beaufort West Area. Explanation to Sheet 3222. 1: 250 000.* Pretoria: Government Printer.

KING, L. C., 1942. *South African Scenery*. London: Oliver & Boyd.

KNIGHT, D.H. 1987. Parasites, lightning, and vegetation mosaic in wilderness landscapes. Pp. 59-83. *In:* TURNER, M.G. (ed.). *Ecological Studies 64. Landscape Heterogeneity and Disturbance.* New York: Springer-Verlag.

KRUGER, G.P. 1983. *Terrain morphological map of southern Africa*. Pretoria: Soils and Irrigation Research Institute.

LAND TYPE SURVEY STAFF. 1993. Land types of the maps 3222 Beaufort West. *Memoirs on the Agricultural Natural Resources of South Africa* 16.

LE HOUÉROU, H.N. 1989. The grazing land ecosystems of the African Sahel. *Ecological Studies* 75. Berlin: Springer-Verlag.

MOLL, E.J. & F. WHITE. 1978. The Indian Ocean Coastal Belt. Pp. 463-515. *In:* WERGER, M.J.A. (ed.). *Biogeography and Ecology of Southern Africa*. The Hague : Junk.

MOORE, A. 1989. Die ekologie en ekofisiologie van *Rhigozum trichotomum* (Driedoring). Ph.D thesis, University of Port Elizabeth, Port Elizabeth.

MUELLER-DOMBOIS, D. & H. ELLENBERG. 1974. *Aims and methods of vegetation ecology*. New York: John Wiley.

NOY-MEIR, I. 1982. Stability of plant-herbivore models and possible applications to savanna. Pp. 591-609. *In*: HUNTLEY B.J. & B.H. WALKER (eds.). *Ecology of tropical savanna*. Berlin: Springer-Verlag.

PALMER, A.R. 1989. The vegetation of the Karoo Nature Reserve, Cape Province. I. A phytosociological reconnaissance. *South African Journal of Botany*. 55: 215-230.

PALMER, A.R. 1991a. A syntaxonomic and synecological account of the vegetation of the Camdebo and Sneeuberg regions of the Nama-Karoo biome, South Africa. *South African Journal of Botany* 57(2): 76-94.

PALMER, A.R. 1991b. Vegetation/environment relationships in the central area of the Cape midlands, South Africa. *Coenoses* 6(1): 29-38.

ROUX, P.M., C.D. KOTZE, G.P. NEL & H.F. GLEN. 1994. *Bossieveld. Grazing plants of the Karoo and karoo-like areas*. Cape Town: Department of Agriculture, South Africa. (Bulletin 428).

ROUX, P.W. & D.P.J. OPPERMAN. 1986. Soil Erosion. Pp. 92-111. *In:* COWLING, R.M., P.W. ROUX & A.J.H. Pieterse (eds.). *The Karoo Biome: a preliminary synthesis. Part I - physical environment.* Council for Scientific and Industrial Research, National Programmes Unit. (South African National Scientific Programmes report; no 124).

ROUX, P.W. & M. VORSTER. 1983. Vegetation change in the Karoo. *Proceedings of the Grassland Society of southern Africa* 18: 25-29.

RUTHERFORD, M. C. & R.H. WESTFALL. 1986. Biomes of southern Africa - an objective categorization. *Memoirs of the Botanical Survey of South Africa* 54: 1-98.

SCHOFIELD, C.J. & E.H. BUCHER. 1986. Industrial contributions to desertification in South America. *Trends in Ecology and Evolution* 1: 78-80.

SCHULZE, B.R. 1947. The climate of South Africa according to the classification of Koppen and Thornthwaite. *South African Geographical Journal* 29: 32-42.

SHEARING, D. 1994. Karoo. *In*: LE ROUX, A. (ed.). *South African Wild Flower Guide 6*. Cape Town: Botanical Society of South Africa.

SHMIDA, A. 1985. Biogeography of desert flora. Pp. 23-73. *In:* EVENARI, I., NOY-MEIR, M. & GOODALL, I. (eds.). *Hot deserts and arid shrublands*. Amsterdam: Elsevier.

SCHMIDT, A.G. 1992. Guidelines for the management of some game ranches in the Mixed Bushveld communities of the north-western Transvaal, with special reference to Rhino Ranch. MSc (Wildlife Management) thesis, University of Pretoria, Pretoria.

SOUTHWOOD, T.R.E. 1978. *Ecological Methods*. London: Chapman and Hall.

STATGRAPHICS. 1989. Statistical Graphics System by Statistical Graphics Corporation. Maryland.

TAYLOR, C.A. & M.H. RALPHS. 1992. Reducing livestock losses from poisonous plants through grazing management. *Journal of Range Management* 45: 9-12.

VAN ROOYEN, N. 1978. 'n Ekologiese studie van die plantgemeenskappe van die Punda Milia-Pafuri-Wambiyagebied in die Nasionale Kruger Wildtuin. M.Sc (Wildlife Management) thesis, University of Pretoria, Pretoria.

VORSTER, M. 1985a. The influence of climate on vegetation in the Karoo: six veld types at Grootfontein College of Agriculture. *Abstract in Agricultural Research* : 79-80.

VORSTER, M. 1985b. Die ordening van die lantipes in die Karoostreek in redelike homogene boerderygeboede dur middel van plantegroei- en omgewingsfaktore. D.Sc thesis, Potchestroom University for Christian Higher Education, Potchefstroom.

VORSTER, M. & P.W. ROUX. 1983. Veld of the Karoo areas. *Proceedings of the Grassland Society of Southern Africa* 18: 18-24.

WALTHER, H. & H. LIETH. 1960. *Klimadiagramm - Weltatlas*. Jena: Fischer.

WERGER, M.J.A. 1974. On concepts and techniques applied in the Zurich-Montpellier method of vegetation survey. *Bothalia* 11: 309-323.

WERGER, M.J.A. 1978a. Biogeographical division of southern Africa. *Monographical Biological* 31: 147-170.

WERGER, M.J.A. 1978b. The Karoo-Namib Region. *Monographical Biological* 31: 231-299.

WERGER, M.J.A. & B.J. COETZEE. 1978. The Sudano-Zambezian Region. Pp. 301-462. *In:* WERGER, M.J.A. (ed.). *Biogeography and Ecology of southern Africa*. The Hague: Junk.

WESTHOFF, V. & E. VAN DER MAAREL. 1973. The Braun-Blanquet approach. Pp. 287-399. *In:* WHITTAKER, R.H. (ed.). *Handbook of vegetation science*. The Hague: Junk.

WESTOBY, M., B.H. WALKER & I. NOY-MEIR. 1989. Opportunistic management for rangelands not at equilibrium. *Journal of Range Management* 42: 266-274.

WHITE, F. (ed.). 1983. *Vegetation of Africa*. Paris: UNESCO/AETFAT/UNSO.