The physical environment and major plant communities of the Tankwa-Karoo National Park

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Apart from Acocks (1988) there are no published descriptions of the vegetation of the greater Tanqua and Doring River drainage basin (Bayer *et al.* 1993). A botanical and physical description of the Tankwa-Karoo National Park (TKRNP) which occurs in Veldtype 31b (Acocks 1988) is provided. The three dominant geological formations, older glacigenic deposits of the Dwyka Group, followed by the succession of siliciclastic sediments of the Permian Ecca Group, with flat dolerite sills and dykes, underlie eight distinct plant communities. The plant communities can be divided into large open plains dominated by *Galenia africana* and *Tripteris* sp. in the erosion rills, *Malephora luteola* and *Augea capensis* common in the low lying areas and *Zygophyllum microcarpum*, *Brownanthus ciliatus* and *Galenia crystallina* common on the more shaly concave plains and low shale hills. Slightly elevated rocky areas are dominated by *Ruschia* cf. *robusta*, *Ruschia spinosa* communities, while crusts of stemless mesembs such as *Rhinephyllum macradenium*, *Hereroa fimbriata* and *Cheiridopsis acuminata* are found on the desert paved areas. Annual Asteraceae covers all the denuded and sparsely vegetated areas after good winter rains while annual mesembs colonise on the more sodic sites. A total of 259 plant species were collected sporadically over a period of eight years, this includes 65 succulents and seven species endemic to the Tanqua Karoo and immediate adjacent area of the Roggeveld Mountain Range and Sutherland. Four Tanqua Karoo endemic species were found in the park.

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Introduction

The succulent Karoo biome has been identified as a major conservation priority (Siegfried 1989; Hilton-Taylor & Le Roux 1989; Cowling & Hilton-Taylor 1994; Rebelo 1994) with only 2,82 % conserved (Low & Rebelo 1996). In the latest estimates of number of taxa in the succulent Karoo flora, a total of 5 183 taxa were counted, 2 134 (41.2 %) of which are endemic (C. Hilton-Taylor *pers.comm.*) in 1 212 km² (Rutherford & Westfall 1986). This region is generally considered to be under-collected, with plant distribution ranges poorly documented and the taxonomy of its most diverse groups, particularly Mesembryanthemaceae requiring major revision (Milton *et al.* 1997). It is still however considered to have the highest species richness recorded for arid vegetation (Cowling *et al.* 1989).

The TKRNP originally consisted of eight government farms, leased to farmers for small stock farming. In 1984 the Department of Nature and Environmental Conservation, of the Cape Provincial Administration, investigated the possibility of converting this area into a Provincial Nature Reserve. This proposal was rejected after an evaluation indicated a low conservation potential for the area (Le Roux & Lloyd 1984). Hilton-Taylor & Le Roux (1989) also assigned a low conservation priority rating to the Tanqua Karoo and Roggeveld, based on number of threatened taxa, compared to the rest of the succulent Karoo. Nevertheless in 1985 the National Committee for Nature Conservation

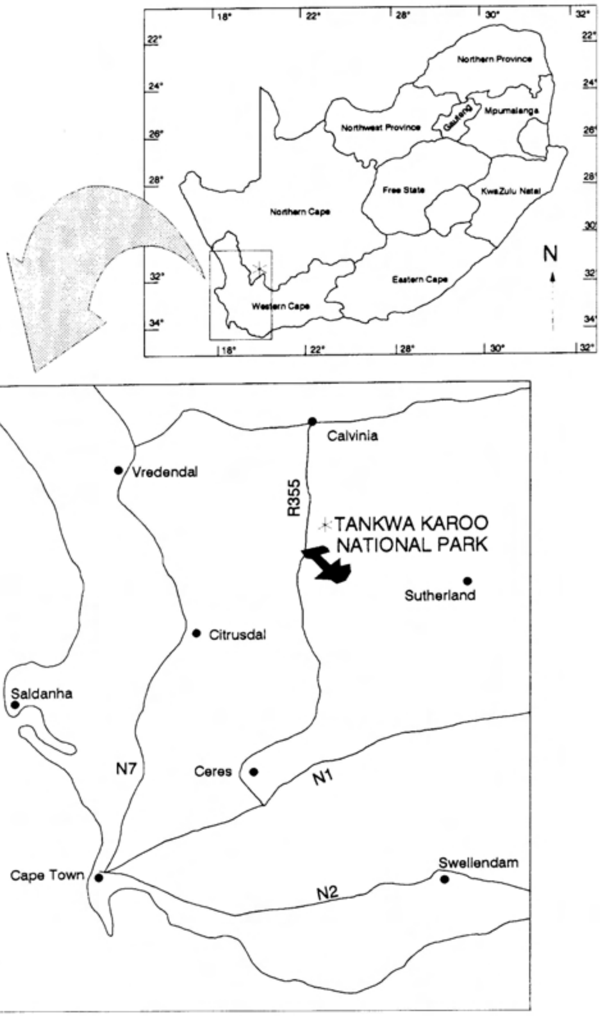


Fig. 1. Map showing the locality of the Tankwa-Karoo National Park.

(NAKOR), which consisted of representatives of various government, semi-government, and provincial authorities involved in land issues, proposed that this area be proclaimed a national park. The Tankwa-Karoo National Park, comprising 27 064 ha was established the following year (Government Gazette NR. 10442 of 19 September 1986).

Apart from Acocks (1988) there are no published descriptions of the vegetation of the greater Tanqua and Doring River drainage basin (Bayer *et al.* 1993). The purpose of this survey was to supply more information with respect to the physical environment, the phytosociology, a species checklist, and biodiversity of the various plant communities in the TKRNP. This information will, allow comparisons with neighbouring areas, as more data becomes available.

Study area

The Tanqua Karoo region is situated between the Cedarberg Mountains in the west, the

Roggeveld escarpment to the east and the Klein Roggeveld Mountains to the southeast. The TKRNP (32°10'S–32°23'S, 19°41'E–19°58'E) is situated in the northern section of the Tanqua Karoo, some 110 km north of Ceres and 90 km south of Calvinia (Fig. 1).

History

Nomadic pastoralism first brought sheep into the succulent Karoo about 2 000 years ago, and cattle some 1 500 years later. The European pastoralists (trekboere) who moved northwards from the Cape Peninsula in the 18th century were nomadic, moving with their flocks to suitable grazing. Sheep farmers moved into the Roggeveld area in the mid-eighteenth century (Calvinia Museum *pers. comm.*). In the 19th century the succulent Karoo became the first biome used for settled European pastoralism (Milton *et al.* 1997).

The extremely arid summers however make much of the succulent Karoo unsuitable for settled pastoralism, even now when boreholes provide perennial water and forage can be imported from other areas (Milton *et al.* 1997). Boreholes initially made more areas available to livestock, but currently stocking-rates in the succulent Karoo are inversely related to water-point density, suggesting that untapped forage reserves, far from natural surface water, have now been depleted (Dean & Macdonald 1994).

Accelerated erosion probably started actively in the Tanqua Karoo as early as the beginning of the 19 th century. The rapidly expanding stock farming industry was compelled to open up new grazing fields for the growing numbers of sheep in the Karoo (Roux & Opperman 1986). Increases in toxic perennials and reductions in forage plants (Beukes *et al.* 1994) necessitated a reduction of 75 % of domestic livestock between 1850 and 1980 (Milton *et al.* 1997). A common practice, which is still used, is to move the small stock from the Sutherland district down into the Tanqua Karoo for 4–5 months, during the winter season.

Climate

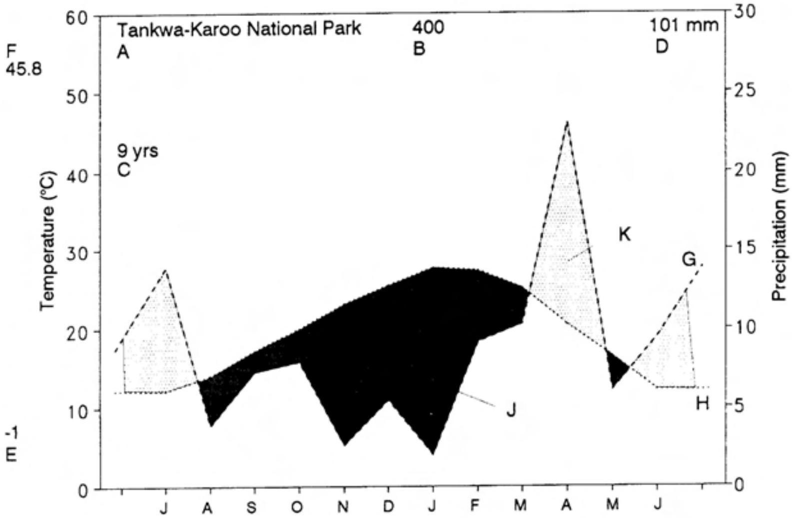
The duration and temperature of the growing season clearly separates succulent Karoo (short, cool) from other biomes, e.g. fynbos (long, cool), Nama-Karoo (short, warm), and savanna (long, warm) (Ellery *et al.* 1991). The Tanqua Karoo is one of the most arid sections of the Karoo. Isohyets of mean annual rainfall (mm) for the Karoo indicate that the TKRNP falls into the 0–100 mm range (Venter *et al.* 1986), with 25 % of the mean annual precipitation falling in summer.

Mean annual precipitation measured over a nine-year period (1987–1995) was 101 mm (Fig. 2), with only 70.8 mm for 1992, 44.9 mm for 1994, and 79.5 mm for 1995. Mean monthly rainfall was highest during April (23 mm) and lowest for January (2 mm). The mean July minimum temperature is 5.7 °C, and the mean January maximum temperature is 35.9 °C. The highest average maximum temperatures and wind speeds occur from November to March and from October to March respectively.

Geomorphology and physiography

The Doring and Tanqua Rivers, which mainly rise in the Klein Roggeveld region, drain the Tanqua Karoo. These rivers are non-perennial, experiencing occasional floods during heavy rainstorms (De Villiers Wickens 1994).

The largest section of the TKRNP consists of long gentle slopes with regular erosion rills fanning out from about 488 m above sea level in the Potkleiberg South section of the park (Fig. 3), towards the lower plains in the Springbokfontein and Springbokvlakte section of the park (350 m). The following features provide topographical diversity: five prominent hills and a ridge (Leeuberg, Pramberg, Potkleiberg, Bloukop, Platkop and Koelandsrug); Kimberlite hills; six springs (spread out in the park); the low-lying alluvial floor at 366 m altitude in the northern section of the park (Fig. 3); various floodplains; and drainage lines of greater or



A = Name of Station
B = Altitude (m)
C = Number of years of observation
D = Mean annual precipitation
E = Absolute minimum temperature (°C)
F = Absolute maximum temperature (°C)
G = Curve of mean monthly precipitation
H = Curve of mean monthly temperature
J = Dry period
K = Wet period

Fig. 2. Climate diagram for the Tankwa-Karoo National Park.

lesser proportions. Leeuberg at 733 m is the highest hill.

A flat dolerite plateau in the central narrow section of the park provides the only grassy plains. Steep white shale slopes separate this elevated dolerite plateau from the rest of the park. North of this plateau, a broken terrain consisting of several low rolling hills is found, which in turn gives way to lower undulating black plains. Thin layers of desert pavement gravel cover these lower undulating plains, with large areas denuded of any vegetation. Drainage lines intersperse these broken terrains giving rise to larger floodplains lower down.

The Tanqua River flows south of the southern boundary of the park, where a large man-made dam provides water for large-scale flood irrigation farming.

Geology

The 1:250 000 scale geological map of the Clanwilliam district (3218 Clanwilliam Geology map) was used to describe the geology of the park.

Approximately 30 % of the park in the north, north-western section, consists of the older glacigenic deposits of the Dwyka Group. Siliciclastic sediments of the Permian Ecca Group stratigraphically follow the above in the central, eastern and southern section of the park (De Villiers Wickens 1994). De Villiers Wickens (1994) describes the Ecca

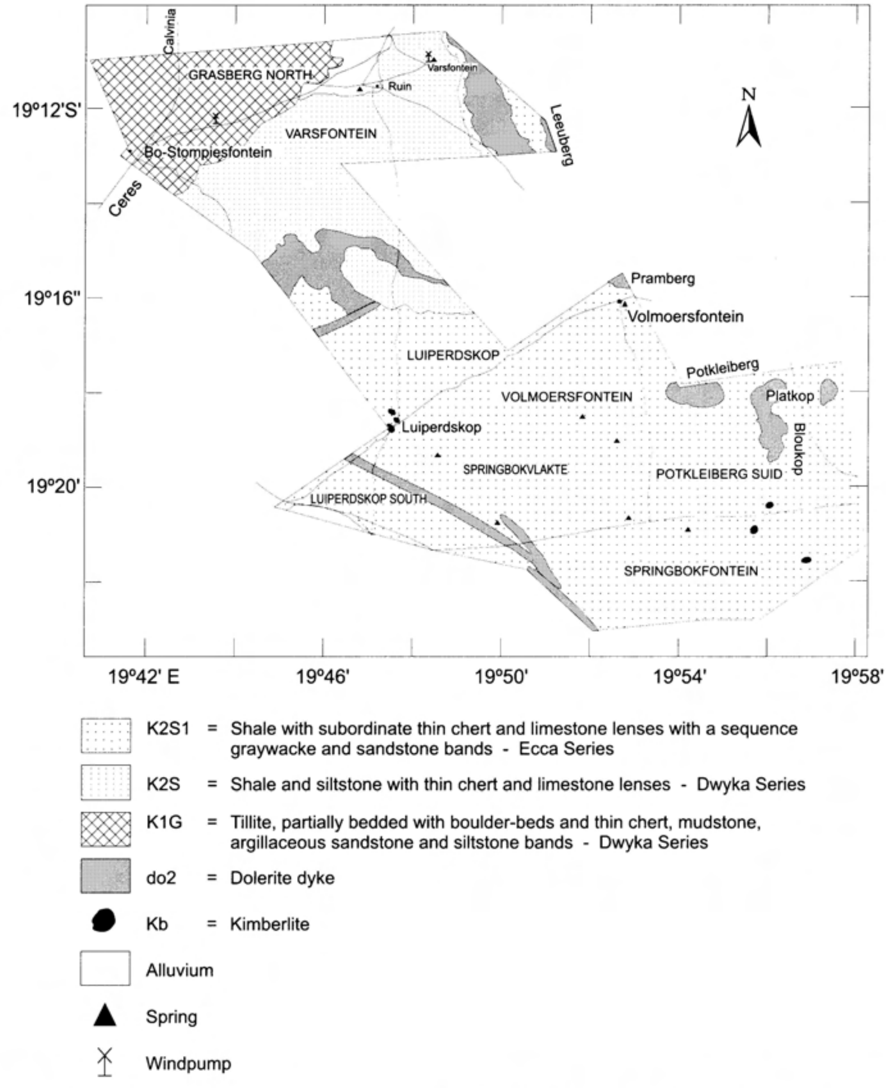
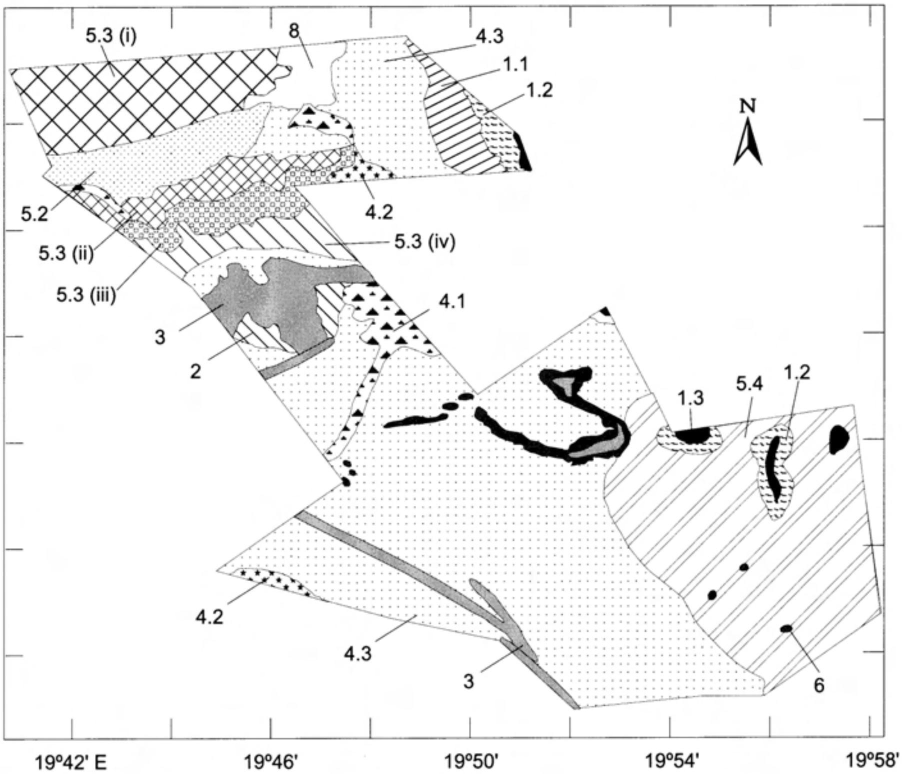


Fig. 3. The geology of the Tankwa-Karoo National Park, including the principle areas and features (3218 Clanwilliam Geology Map).

strata as representative of a period of basin filling that commenced with transgressive post-glacial flooding of large parts of southwestern Gondwana in the early Permian, through a phase of deep water deposition, to a final regressive phase of deltaic build-out into the basin.

The Dwyka tillites consist of a mixture of ancient till deposits preserved and compacted in hard rock called tillite (King 1963). The sedimentary rocks of the Ecca and Dwyka shale's, are derived from erosion of previously existing rock, transported by water and deposited in flat-lying strata of mud which gives rise to shale.

Dolerite sills occur on the flat tops of hills and on a lower plateau in the central section of the park (Grasberg). A narrow dolerite dyke is also visible in the southern section of Springbokvlakte.



1.1 The *Tylecodon wallichii - Euphorbia hamata* Succulent Dwarf Shrubland.

1.2 The *Monechma spartioides - Tripteris sinuata* Dwarf Shrubland.

1.3 The *Euphorbia hamata - Ruschia spinosa* Dwarf Shrubland.

2. The *Stipagrostis ciliata - Salsola aphylla* Grassland.

3. The *Ruschia wittebergensis - Salsola aphylla* Dwarf Shrubland.

4. The *Lycium cinereum – Malephora luteola* Plains.

4.1 The *Salsola aphylla - Lycium cinereum* Shrubland.

4.2 The *Cladoraphis spinosa - Lycium cinereum* Sandy Floodplain.

4.3 The *Zygophyllum microcarpum - Lycium cinereum* Open Plain.

5.1 [1]The *Drosanthemum delicatulum - Ruschia spinosa* Dwarf Shrubland.

5.2 The *Rhinephyllum macradenium - Ruschia spinosa* Succulent Dwarf Shrubland of the low-lying Dwyka shale desert paving.

5.3 The *Cheiridopsis acuminata - Ruschia spinosa* Dwarf Shrubland of (i) the Dwyka tillite, (ii) undulating Dwyka shale hills, (iii) sharply undulating black desert paving area, and (iv) a narrow even sloped area paved with red-black sandstone stones.

5.4 The *Tripteris sinuata - Ruschia spinosa* Dwarf Shrubland.

6. The *Brownanthus ciliatus - Enneapogon scaber* Dwarf Shrubland.

7. [1]The denuded to bare areas on desert paving gravel and shale hills.

8. Alluvial floors.

[1] Not indicated on map

Fig. 4. A vegetation map of the dominant plant communities of the Tankwa-Karoo National Park.

Metamorphism of mudstone and limestone is particularly visible near the flat dolerite plateau, where pressure and temperature altered mudstone, slate, hornfels and schist (Mountain 1968). Rainwater readily acts on limestone, bearing carbon dioxide in solution. In these arid areas, where it is relatively free from chemical attack, limestone proves to be a moderately resistant rock (King 1963). Greywacke and sandstone bands are also visible surrounding the dolerite in this central section (3218 Clanwilliam Geology map).

Shallow depressions, consisting of muddy and salty accumulation, form alluvial floors, some of which occur, along the central section of the northern boundary. These floors are mainly due to wind action: water in the past collected in slight hollows, causing local, more concentrated disintegration of the underlying sandy or shale rock. When the water evaporates in the dry season, the wind carries away the disintegration products, thus lowering the levels of the floors very slightly. With repetition, huge floors form that sometimes coalesce (King 1963). Streams which enter bring salts in solution, which adds to the decay of the bedrock.

Land type mapping and soils

The Land Type Survey Staff (1996) produced a land type classification for the park. The various land type units were Ms1, Ms2, Ms3, R1, R2 and Oa1. Ms1 occurs predominantly on the crest of the Dwyka tillite section (Fig. 3), and consists of shallow soils with underlying rock, weathered rock or hardpan calcrete. Ms2 occurs predominantly on the slopes of the Dwyka tillites (Fig. 3), with underlying shale of the Dwyka Group. Soil forms are predominantly Mispah, Hutton and Glenrosa. Land type Ms3 occurs in the open plains, with shallow soils, predominantly Glenrosa soil form, with underlying shale and siltstone from the Ecca Group (Fig. 3). Land type R1 describes the dolerite plateau and limestone lenses in the central section of the park (Fig. 3), while land type R2 describes the various prominent hills. Land type Oa describes the floodplain and alluvial floor that occurs in the northern section of the park. The underlying geology is alluvium with tillite of the Dwyka Group and shale and siltstone from the Ecca Group.

Central Agricultural Laboratories, analysed soil samples collected in selected relevés. Both the soil sample analyses results and the land type descriptions were used to assist in the habitat description of the plant communities.

Vegetation

Acocks (1988) described the Tanqua Karoo (VT 31b) as "terribly tramped out, and eroded down to the bare shale". The better conserved sections he described as a short succulent Karoo with many of the mesembs being of the stemless type; with non-succulents also found, and *Stipagrostis obtusa*, even becoming abundant after good rains. Annuals and geophytes are numerous but rarely seen (Acocks 1988).

Milton *et al.* (1997) describe the vegetation structure of VT 31b as very sparse Shrubland and Dwarf Shrubland (< 0.3 m), with succulents on shallow soils, and grass and ephemerals on sandy alluvium. The dominant taxa of these areas are, succulents: *Augea*, *Cephalophyllum*, *Crassula*, *Pleiospilos*, *Psilocaulon*, *Hereroa*, *Rhinephyllum*, *Ruschia*, *Sphalmanthus*, *Sceletium*, *Tetragonia*; and non-succulents: *Acacia karroo*, *Galenia*, *Hermannia*, *Lycium*, *Osteospermum*, *Pteronia*, *Salsola*, *Stipagrostis*, *Tamarix* and *Zygophyllum*.

Methods

Methods and techniques of the Zürich-Montpellier school (Westhoff & Van der Maarel 1973; Mueller-Dombois & Ellenberg 1974; Werger 1974) were applied in this study. Stratified random sampling was used to select 98 sampling sites. The study area was subjectively divided into communities (Figs. 4&5) based on stratification of aerial photographs, topographical position, aspect and geology.

Table 1

A phytosociological table of the Tankwa-Karoo National Park

Community number	1.1	1.2	1.3	2	3	4.1	4.2	4.3	5.1	5.2	5.3	5.4	6	7
	1					4			5					
Releve number	7889 9016	8919179 2824383	89797 37756	8922666 8194789	55555 20413	587789789 892340072	2272 6741	2333334444 0567890123	3333138 0234416	2 1562423	6567644464555 5931448526567	6 7 1 078591	1111122 7856985	6846421 1576930
SPECIES GROUP A														
Euphorbia hamata	+R+	+ R+++	++ ++						R					
Euphorbia decussata	+++	+	++									+		
Pteronia pallens	M M	+	A		+	+		R	R					
Felicia lasiocarpa	M	+ +	+											
Pentzia incana		+	++											
Pteronia viscosa		M	+											
Drosanthemum hispidum			M										R	
Dipcadi brevifolium	+		+											
Pelargonium magenteum	R	+R												
Microloma saggitatum		R	R											
SPECIES GROUP B														
Tylecodon wallichii	+++M	+												
Lampranthus diffusus	B B												+ M	
Pteronia villosa	+M					+								
SPECIES GROUP C														
Monechma spartioides		M++MA M	++										R	
Sericocoma avolans		+ + +												
Pteronia mucronata		++ +												
Asparagus capensis		R R++	+						R					
Hermannia spinosa		+ +												R
Pteronia scariosa		+ R		R										
Pteronia leucoclada		A												
Hirpicium alienatum		+												
Stapelia sp.		R R												
Haworthia sp.		R												
SPECIES GROUP D														
Stipagrostis ciliata		+ R		M+BAAMM		+ +		+						
Salsola cryptoptera				+ RM										
Babiana truncata				R R										
Lebeckia spinescens				A										
Melolobium exudans				M										
Salsola zeyheri				M										
Stipagrostis namaquensis		R		M					R					
SPECIES GROUP E														
Bulbine alooides					++R +						R			+
Ruschia wittebergensis					+++					+	R			
Pteronia glabrata	M	R+			+ R +	+		R						
Pteronia lucilioides					++									
Gnidia polycephala					+ +									
Jamesbrittenia atropurpurea					++									
Berkheya spinosa			++		++	+								
Thesium lineatum		+			RR									
Moraea speciosa					R R							R		R R
SPECIES GROUP F														
Lycium cinereum	+		+		R +	R M R R	M++	RR+R+RR++			+	+	+	R
Malephora luteola				+		M M	++++	+MR R R	+ +	A	+			

Table 1
(continued)

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SPECIES GROUP G
Drosanthemum wittebergense           |    |       | M   |       |      | M+      |    |          |       |       |           RR |      |       |       |
Eriocephalus capitellatus            |    |       |  +  |       |      | ++      |    |          |       |       |              |      |       |       |
Drosanthemum subcompressum           |    |       |     |       |      | ++      |    |          |       |       |              |      |       |       |
Psilocaulon cf. pageae               |    |       |     |       |      | R+      | +  |          |       |       |              |      |       |       |
Tetragonia sarcophylla               |    |       |     |       |      | M       |    |          |       |       |              |      |       |       |

SPECIES GROUP H
Cladoraphis spinosa                  |    |       |     |+      |      |         |MM+ |    R     |       |       |              |      |       |       |
Salsola contrariifolia               |    |       |     |       |      |         |MM R|          |       |       |              |      |       |       |
Lotononis pungens                    |    |       |     |    +  |      |         |++  |          |       |       |              | ++   |       |       |
Ornithogalum xanthochlorum           |    |       |     |    +  |      |         |R+  |          |       |       |              |      |       |       |

SPECIES GROUP I
Salsola aphylla                      | +  |       |     |M    MAM|MM+ +|++A++++++| A  |          |       |       | R          R |      |       |       |
Psilocaulon absimile                 |    |       |    +|   R   |R  R+|       R |++  |          |       |       |      R       |      |       |       |
Lotononis densa subsp. gracilis      |    |       |     | +   ++|  +++|    +    |    |          |       |       |              |      |       |       |
Tripteris oppositifolium             |    |       |     | +     | + + |++A      |   +|          |      +|       |          +   |+     |       |       |
Zaluzianskya mirabilis               |    |   +   |     |R     R|     |       + |    |          |       |       |              |      |       |       |
Zygophyllum retrofractum             |    |       |  +  |    R  |     |         |   +|          |       |       |              |      |       |       |

SPECIES GROUP J
Ruschia spinosa                      |    | +    M| +++ |       |      | +       |    |          |++MA + |  MB R|+MM MMMM +   |  MM+A|       |       |
Ruschia cf. robusta                  |    |       |     |       |      |         |    |          |++MR M | BB    |++M  AA MA    | B ++ |       |       |
Galenia fruticosa                    |    |    +  |  +  | +M    | +R   |+     +  |    |   RR     | RRR R |++ BM  | ++++         |  +   |       |       |
Drosanthemum eburneum                |   R|       |     |       |      |         | R  |          |A+M  M |R  M++ |      R    BA+|      |     M+|       |
Pteronia intermedia                  | M  |       |     |       |      |         | +  |          |     + |  +R+  | R     R    R |      |    +  |       |
Crassula subaphylla                  |+ + |       |  +  |       |      |         |    |          |       | R     |      R       |R  R  |       |       |
Crassula muscosa                     | +  |       |     |       |      |         |    |          |       |+R R   |       R   R  |+ R R |       |       |
Euphorbia restituta                  |    |R    + |     |       |R     |         |    |          |       |       |          R   | +R   |       |       |
Sarcocaulon crassicaule              |    |       |     |       |R     |         |    |          |      R|       |      +       |      |       |       |
Lyperia tristis                      |    |       |     |R      |      |         |    |          |       |      R|          R   |      |       |       |
Sarcocaulon salmoniflorum            |    |       |     |       |      |         |    |          |       |       |      R       |      |       |       |

SPECIES GROUP K
Aridaria sp.                         |    |       |     |       |      |         |    |          |M  + + |       |              |      |       |       |
Psilocaulon utile                    | +  |       |R    |   R   |      |        +|    |         R|+R + R |       |              |      |       |       |
Pteronia punctata                    |    |       |     |       |      |         |    |          |+ +  + |       |              |      |       |       |
Cephalophyllum ebracteatum           |    |       |     |       |      |         |    |          | R+  M |       |         +    |      |       |       |
Drosanthemum delicatulum             |    |       |     |       |      |         |    |          |R++    |       |              |      |       |       |
Leipoldtia schultzei                 |    |       |     |       |      |         |    |          | + +   |       |              |     A|       |       |
Drosanthemum lique                   |    |       |     |       |      |+        |    |          | ++    |       |              |      |      B|       |
Crotalaria sp.                       |    |       |     |       | +    |         |    |          |    + R|       |              |      |       |       |
Drosanthemum cymiferum               |    |       |     |       |      |         |    |          | R  +  |       |              |      |       |       |
Galenia secunda                      |    |       |     |       |      |         |    |          |+    R |       |              |      |       |       |

SPECIES GROUP L
Salsola calluna                      |    |       |     | A     |      |         |    | RR+  +RR| +M  + |       |              |      |       |       |
Drosanthemum sp.                     |    |       |     |       |      |         | +  | R      R|MMR  + |R      |              |      |       |       |
Salsola glabrescens                  |    | R     |     |       |      |         |    |R + MR   | +R    |       |              |      |       |       |

SPECIES GROUP M
Aridaria noctiflora                  |    |R +    |     |RMM +++|M++   |+  ++   +| +++|  R +     |M+RMM  |  +    |    +         |      | ++  + |  +    |
Zygophyllum microcarpum              |    |R+ +   | R+  |+++    |+  ++ |+   + ++ |    |+R+MR+++M+| R +M +|       |              |  +   |       | +     |
Eriocephalus spinescens              | ++ | + +   |     | + M   |+  +  |      +  |    |      R   |     + |       |              |      |+      |       |
Trichodesma africanum                |    |       |    +|R      |     R| +       |    |+R R   RR|      +|       |              |      |R      |       |
Lycium ferocissimum                  |  R |       |     |     R |R     |         |  A |          |       |       |              |      |       |       |
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Table 1
(continued)

SPECIES GROUP N														
Rhinephyllum macradenium									R	++ R				
Bulbine sp.										+ ++				
Tripteris clandestina										++ +				
Heliophila deserticola		+								+ R+ R		+		
Arctotis laevis										+ + R				
Dipcadi crispum										+R+				
Ruschia sp.										B +				
Eurystigma clavata										M+				
Bassia salsoloides										R M				
Salsola rabiena										M				
SPECIES GROUP O														
Augea capensis	+R+M			+		++ +++	+ +R	AM+MM+MMM	+++R M	A R R++	RR		+	R
Lessertia pauciflora var. pauciflora				M			++	R		+ + +				
SPECIES GROUP P														
Cheiridopsis acuminata											R M M+			
Osteospermum pinnatum var. pinnatum								R		+	+ +M ++R		+ +	
Heliophila digitata	+		+ +	+					+		++ ++			++
Mesembryanthemum cf. nodiflorum										+	M M			A+ +
Mesembryanthemum sp.					+					B	+ + +			++
Nemesia ligula											R+ +			+
Hereroa fimbriata											+ +			
Hebenstretia parviflora											+ +			
Mesembryanthemum cf.stenandrum			+				+				R+			R
SPECIES GROUP Q														
Tripteris sinuata	RM	+M+M+	++	++RM +		+ +	+ M	+MR RRR	R MMR	R	+	++RR+	M+++	R
Stipagrostis obtusa		+	+	M M+ +	++	+	A	+M+ MMM+RR	R +	M +	R	+ R R	+RRR	
Galenia africana		+MM		+	+	M	+	RR+ R R	+++MMR+	MR		++A RM	M B	
Enneapogon scaber		+M + +M	+			+ R			+			+	MA+++ +	
Galenia crystallina	++	+ +	+	+		++	R			R	+	R	RMM M	
Atriplex lindleyi subsp. inflata	+			R		+ R	R	RR	++	+ + R		R	++M+	
Amellus tridactylus		+					++ +	R	+	++ R		R R+	++RR +	R
Brownanthus ciliatus		M	+		+	+	+		+ M	R ++	+		A MM	+
Arctotis hirsuta	+	+ +	+				+		+ R	++ +	+	+ +	B	
Lotononis falcata			+	+									+ + +	
Oxalis pes-caprae		+ +										+	+ M +	
Nemesia karroensis				+						R+ R		R	R+	
Oxalis sonderiana			+ +	+		+						+	RR	+
Lasiospermum brachyglossum	+	+								++			+	
Othonna protecta	+									RR			+	
SPECIES GROUP R														
Euryops annuus				+	+++	+ +	M	M +		MR MR	+ ++AM+++M	M A A	M+ M +	+A+MM
Gazania lichtensteinii		+ R+++	+	+		+ R	+ +	R +	+	+MM+ +	A ++ +	M++++	++++++++	+ + R
Tetragonia echinata			A	+ ++		++				+++ R	M++M + ++++	+ + +	++	M+
Ursinia nana	+ +	+		+ ++		++				++ +	M++M +	+	+ + +	A+
Oncosiphon grandiflorum		+					++		+	RRR+RM	M +	+	+R+ A++	+ +
Tetragonia fruticosa	M	++ +		R	R ++	+	R		++		+ R	+M	++	
Lapeirousia pyramidalis					+RR	R					+R +			
Mesembryanthemum crystallinum	+ +	+	++ +			+ +	+		R +	+ +	+ +	RR R		+
SPECIES GROUP S														
Lachenalia mutabilis		R			R	R				+	R R			
Aptosimum indivisum		R				R	+		R	R			R	
Psilocaulon cf. pageae							+			+		+		
Hermannia cuneifolia		+			+	+						+		
Hebenstretia glaucescens													+	

Table 1
(continued)

Crassula deltoidea		R	R						R		R			
Androcymbium capense			R											
Salsola tuberculata		R		+										
Codon royenii			+											
Felicia australis			+										R	
Limeum aethiopicum			R											
Lycium bosciifolium			+											
Oncosiphon pilulifera			+											
Ruschia cf. karooica			+											
Wahlenbergia androsacea		R												
Zygophyllum meyeri			+											
Albuca maxima		R												
Aridaria sp.		R												
Forsskaolea candida		+												
Lachenalia anguinea			R											
Cyanella hyacinthoides			R			R								
Hermannia incana				R										
Lachenalia violacea						R								
Lessertia annularis						R								
Massonia depressa						R								
Melolobium microphyllum						R								
Moraea crispa				R										
Ornithogalum secundum						+								
Othonna pteronioides						R								
Salvia disermas						R								
Senecio elegans						+								
Sutherlandia microphylla						R								
Aridaria sp.									+					
Bromus pectinatus	+													
Othonna arbuscula		+										R		
Senecio cardaminifolius												R		
Ruschia cf. herrei	R													
Galenia sarcophylla	+						+							
Crassula umbellata	R													
Mesembryanthemum pachypus	+													
Senecio arenarius			+							+				
Berkheya fruticosa		R											+	
Manulea cf. latiloba										R				
Rhus undulata													+	
Selago albida		+											+	
Plinthus karooicus											R			+
Hypertelis salsoloides						R								
Ornithogalum apertum											R			
Salsola cf. dealata											+			
Senecio cakilefolius														+
Gethyllis cf. verticillata											R			
Lapeirousia plicata											+			
Albuca cooperi												+		
Albuca sp.											R			
Zaluzianskya bella												+	R	
Zygophyllum sp.		+								+		+		
Lophochloa pumila										+			+	

Table 2
Soil sample analyses

Com-munity	Relevè	pH (KCl)	Cmol	P	K (mg/kg)	Ca (mg/kg)	Mg (mg/kg)	Na (mg/kg)	Mn (mg/kg)	Cu	Zn	Ohm	Clay%	Silt %	Sand %	Texture
2	67	8.2	0	2	212	1743	130	28	11.5	0.6	0.6	2600	6	1	93	B-LmSa
	68	7.9	0	5	138	1920	97	90	11.4	0.6	0.4	2500	10	4	86	B-LmSa
	69	7.9	0	4	141	3118	134	67	11	0.6	0.5	2400	8	5	87	B-SaKlLm
3	52	8	0	4	264	3196	287	195	12.6	0.2	0.2	900	18	15	67	B-SaKl
	50	8.2	0	6	215	2850	263	175	0.5	0.2	0.1	650	22	15	63	B-SaKlLm
	54	7.7	0	3	134	22170	231	305	0.6	0.2	0.1	200	67	21	21	B-SaKlLm
4.1	84	5.6	0.3	60	137	1445	855	450	13.3	1	0.8	600	24	5	71	Gr-SaKlLm
	70	8.3	0	4	370	2206	179	1030	34.8	0.7	1.4	240	24	16	60	B-SaKlLm
	87	7.8	0	2	262	3056	167	410	28.4	0.4	0.6	330	32	7	61	Gr-SaKlLm
4.3	42	7.6	0	2	197	1690	100	355	30	0.4	0.6	340	26	2	72	Gr-SaKlLm
5.1	34	4.2	0.8	87	119	488	279	94	18.8	0.5	0.6	1700	18	16	66	B-SaLm
5.3	65	7.8	0	3	210	1450	291	380	156	1.7	3.5	200	26	14	60	B-SaLm
	59	7.5	0	8	414	1450	700	420	28.2	0.9	1.2	460	32	13	55	B-SaKlLm
	63	4	0	30	149	290	394	143	12.5	0.6	0.8	780	20	20	60	B-SaKlLm
	71	8	0	7	379	2677	295	205	22.1	0.9	1.2	470	16	8	76	B-SaLm
	64	3.7	1	32	145	276	347	95	23.1	0.8	0.6	2800	20	19	61	Gr-SaKlLm
	44	7.3	0	7	145	1917	419	345	27	0.7	0.9	220	20	15	65	B-SaKlLm
	48	5.9	0.1	36	109	2048	394	108	17.5	0.6	1.5	700	22	11	67	B-SaKlLm
	45	8.3	0	11	390	2780	255	885	36.6	0.7	1.3	110	16	11	73	B-SaLm
	62	4.8	0.6	79	317	493	580	188	27.1	0.9	1.1	420	26	13	61	B-SaKlLm
	46	6.3	0	40	116	1372	369	135	18.8	0.5	1.4	780	16	10	74	B-SaLm
	55	6.9	0	77	238	1397	382	660	21.5	0.6	0.7	240	24	12	64	B-SaKlLm
	56	6.9	0	65	293	1094	395	370	57.3	0.7	1	360	22	13	65	B-SaKlLm
	57	8.1	0	8	328	2495	280	520	27.1	0.4	0.8	260	24	13	63	B-SaKlLm
5.4	75a	5.8	0.20	220	152	985	246	230	33	0.5	1.2	550	20	9	71	Gr-SaKlLm
	75b	7.9		8	252	2589	174	240	66.2	0.4	1.1	700	20	7	73	Gr-SaKlLm
7	61	6.7	0	220	353	956	750	495	35.1	0.6	1.2	470	32	11	57	B-SaKlLm
	85	7.6	0	12	419	1625	215	111	47.3	0.7	7.2	910	18	9	73	Gr-SaLm
	47	8.1	0	62	402	2790	260	245	53.4	0.4	1.1	660	16	16	68	B-SaLm
	66	7.7	0	26	206	2185	175	445	22.2	0.4	0.4	1000	12	12	76	B-Sa
	49	8	0	4	334	2506	162	390	26	0.6	2	430	20	14	66	B-SaKlLm

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Plot sizes of 10 x 10 m (Palmer 1989) were used in most of the surveys, but larger plots (20 x 20 m) were used in the more denuded areas. In each sample plot, all species were recorded, a percentage projected canopy cover was estimated subjectively for each plant species, and cover-abundance values were allocated according to the scale of Braun-Blanquet (1932), as modified by Werger (1974). 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, to J. Vlok (Cape Nature Conservation, Oudtshoorn), and B. Bayer (Department of Agriculture and Development, Worcester) for identification, and taxon names conform to those of Arnold & De Wet (1993) and other recent taxonomic literature. Environmental variables such as slope, aspect, geology, and rockiness of soil surface were recorded in each sample plot, and summarised for each community after completion of the phytosociological classification.

Data analysis

TWINSPAN (Hill 1974) was used together with the Braun-Blanquet procedure (Bredenkamp *et al.* 1989; Kooij *et al.* 1990) to analyse the raw data, which was then further refined on a spreadsheet (Table 1). Soil samples were collected in the major geological formations, and were analysed for $pH_{(KCl)}$, Na, Ca, Mg, K, total P, Mn, Cu, Zn, soil texture (% sand, silt and clay), and cation exchange capacity, following the standardised methods of ALASA (1990) (Table 2). A global positioning system apparatus was used to record the location (dd:mm:ss) of every sample site.

With the CANOCO package (Ter Braak 1988), correlation-type principle components analysis (PCA) was used to summarize the main patterns of variation in the soil and habitat descriptive variables measured within the study area. A PCA was done on various combinations of environmental and soil analysis data, as redundancy (near linear dependencies) amongst variables were recognized. Variables anallysed were: $pH_{(KCl)}$; resistance (Ohm); persentage sand, silt, and clay; percentage slope; and catenal position. Percentage rock was kept as a passive variable because depth and size of gravel, versus rock, versus desert pavement, often became confusing to classify.

All data were transformed into percentage values, giving each variable equal weighting. In the case of sand, silt and clay, one variable was kept passive because of collinearity. In the presentation of the biplot (environmental variables and sites) (Fig. 6), the increase in abundance (or value of a variable as fitted by PCA) changes linearly across the biplot. The fitted planes in a biplot were represented by arrows, and the direction of the arrows indicated the direction in which the abundance of the corresponding variable increased most, and the length of the arrow equaled the rate of change in that direction. Abundances were constant if a line was perpendicular. The angle between the arrows of a pair of variables indicated similarity in distribution of these variables.

A correspondence analysis (CA) and canonical correspondance analysis (CCA) was done on the vegetation dataset (30 relevés, one outlier relevé was removed) for which soil samples were collected. The vegetation data was simplified by removing all annual and rare species. The CA (Fig. 7) was based on the floristic data alone, with only a passive relation described to the environmental variables. In the case of CCA done on the same floristic dataset, the ordination axes were constrained to linear combinations of the included environmental variables (Witkowski & O'Connor 1996).

The eigen value was equal to the maximum dispersion of the species scores, and was thus a measure of the importance of the ordination axis (Ter Braak 1987b). The eigen value of the first axis was generally the highest, providing the most information, with the subsequent axes and information being of reduced importance.

The CCA ordination, using the sampled topo-edaphic variables, was compared to the CA ordination (Table 3) in order to see if any important environmental variables had been omitted (Witkowski & O'Connor 1996). A Monte Carlo permutation test was then run to determine the significance of the overall CCA ordination and its first axis. This was a direct test to determine if the included environmental variables had a significant effect on vegetation composition.

Biodiversity

The cover-abundance symbols used in the phytosociological table (Table 1) for each species, were converted into mean percentage cover values, for the determination of biodiversity indices (Table 4):

Cover-abundance scale	% Cover ranges	Mean % Cover
R	< 0.1	0.2
+	0.1-0.9	0.6
M	1.0-5.0	3.0
A	5.1-12.0	8.5
B	12.1-25.0	18.5

The Shannon-Wiener species richness, Berger-Parker species evenness, and Margaleff species richness indices were used (Ludwig & Reynolds 1988).

Indices for each relevé were determined separately, as well as for each plant community (adding the various relevés with an average percentage cover-abundance determined for each species). Indices were also determined for the various plant communities excluding the annuals, and for succulents alone (Table 4).

Results and discussion

A phytosociological table, summarising the dominant plant communities is provided in Table 1, and a vegetation map is given in Fig. 4. A preliminary checklist of 259 plant species encountered in the park is presented in Table 5. This includes 38 families and 125 genera. A total of 65 succulent species were collected in the park. Seven species found in the park are endemic to the Tanqua Karoo - Roggeveld mountain area (Vlok *pers. comm*), and four species are endemic to the Tanqua Karoo alone (Hilton-Taylor *pers. comm*) (Table 5). The majority of succulent species are from the families Mesembryanthemaceae, Crassulaceae and Euphorbiaceae.

A summary of the vegetation classification and most prominent determining factors are:

1. The *Euphorbia hamata - Pteronia pallens* Dwarf Shrubland communities of the prominent hills (Leeuberg, Pramberg, Potkleiberg and Bloukop-Platkop):
   1.1 The *Tylecodon wallichii - Euphorbia hamata* Succulent Dwarf Shrubland of the more southwest facing lower slopes of Leeukop.
   1.2 The *Monechma spartioides - Tripteris sinuata* Dwarf Shrubland of the more south facing steep slopes.
   1.3 The *Euphorbia hamata - Ruschia spinosa* Dwarf Shrubland on the dolerite/shale, rocky hilltops.
2. The *Stipagrostis ciliata - Salsola aphylla* Grassland of the dolerite plateau.
3. The *Ruschia wittebergensis - Salsola aphylla* Dwarf Shrubland of the limestone lenses.
4. The *Lycium cinereum – Malephora luteola* Plains communities.
   4.1 The *Salsola aphylla - Lycium cinereum* Shrubland of the more silty drainage lines and floodplains
   4.2 The *Cladoraphis spinosa - Lycium cinereum* Sandy Floodplain community
   4.3 The *Zygophyllum microcarpum - Lycium cinereum* Open Plain community.
5. The *Ruschia spinosa - Ruschia* cf. *robusta* Succulent Dwarf Shrubland communities of the elevated stony areas.
   5.1 The *Drosanthemum delicatulum - Ruschia spinosa* Dwarf Shrubland of the rocky drainage lines.
   5.2 The *Rhinephyllum macradenium - Ruschia spinosa* Succulent Dwarf Shrubland of the low-lying Dwyka shale desert paving.
   5.3 The *Cheiridopsis acuminata - Ruschia spinosa* Dwarf Shrubland of (i) the Dwyka tillite, (ii) undulating Dwyka shale hills, (iii) sharply undulating black desert paving area, and (iv) a narrow even sloped area paved with red-black sandstone stones.
   5.4 The *Tripteris sinuata - Ruschia spinosa* Dwarf Shrubland of the upper slopes of the elongated Ecca plains.
6. The *Brownanthus ciliatus - Enneapogon scaber* Dwarf Shrubland of the Kimberlite hills.
7. The denuded to bare areas on desert paving gravel and shale hills.
8. Alluvial floors.

Plant species in Species Group Q are common to almost the entire park, except for the dense mesemb stands described in community 5.3. These species, particularly common in the plains, include *Tripteris sinuata*, *Stipagrostis obtusa*, *Galenia africana*, *Enneapogon scaber, Galenia crystallina* and *Atriplex lindleyi* subsp. *inflata*. Species Group R contains some of the most abundant annuals that occur throughout the park after good winter rain, with the first five species having a high constancy in communities 5.2

Table 3

Summary of the correspondence analysis (CA) and canonical correspondence (CCA) analyses for the Tankwa-Karoo National Park; a) a CA of the 30 releves where soil samples were collected, axes 1-8, and b) a CCA on the same 30 releves (axes 1-4)

a)	CA - 30 samples, axes 1-4	Axis 1	Axis 2	Axis 3	Axis 4
	Eigenvalue	0.882	0.808	0.640	0.563
	Species-environment correlation	0.656	0.813	0.633	0.658
	Cumulative percentage variance of:				
	Species data	13.4	25.7	35.4	43.9
	Species-environment	15.6	37.6	48.1	58.1
b)	CA - 30 samples, axes 5-8	Axis 5	Axis 6	Axis 7	Axis 8
	Eigenvalue	0,466	0,393	0,361	0,313
	Cumulative percentage variance of:				
	Species data	12,6	23,3	33,1	41,6
c)	CCA - 30 samples, axes 1-4	Axis 1	Axis 2	Axis 3	Axis 4
	Eigenvalue	0.739	0.472	0.399	0.276
	Species-environment correlation	0.950	0.899	0.866	0.834
	Cumulative percentage variance of:				
	Species data	11.2	18.4	24.5	28.6
	Species-environment	30.3	49.7	66.1	77.4

to 7. *Euryops annuus* and *Gazania lichtensteinii* are often found in virtual monoculture stands, providing a spectacular display of yellow flowers in areas which generally appear denuded of vegetation during the summer months. Some of the very common annuals that appear in particular abundance include *Tetragonia echinata*, *Ursinia nana* and *Oncosiphon grandiflorum*. Species Group R appears absent in community 4.3, the largest part of the park, merely because most of these surveys were done in a period when virtually no winter rain fell. Species Groups Q and R are therefore seldom referred to in the rest of the descriptions.

1. The *Euphorbia hamata - Pteronia pallens* Dwarf Shrublands of the prominent hills (Leeuberg, Pramberg, Potkleiberg and Bloukop-Platkop) (Fig. 5a):

All the prominent hills are found in the north-eastern section of the park (Figs. 3, 4 & 5). These hills occur in land type R2 which is described as dolerite with shale and siltstone of the Ecca group consisting mainly of higher hills with steeper middle slopes (Land Type Survey Staff 1996). Leeuberg is the exception, being the largest, with a large lower dolerite section, and occurring in the Dwyka shales.

On the slopes the most common soil forms present are Mispah and Glenrosa, while the crowns of these hills generally have Mispah soil forms (Land Type Survey Staff 1996). The slopes are steep, rocky, and sensitive to erosion, with several erosion gullies visible.

The vegetation is characterised by Species Group A with the diagnostic species, *Euphorbia hamata* and *Felicia lasiocarpa* (when flowering), the most prominent (Table I, Fig. 4). The plant communities are mainly found on the lower southwest facing slopes with dolerite boulders (1.1), on the more south facing steep rocky slopes (1.2), and on the flat hilltops (1.3). These hill communities are the most diverse communities in the park (Table 4), with perennial and succulent species contributing more to diversity than in any of the other communities (Table 4 b&c).

1.1 The *Tylecodon wallichii - Euphorbia hamata* Succulent Dwarf Shrubland of the more southwest facing lower slopes of Leeukop (Fig 4):

This community is found at an altitude of 430–490 m on Leeukop. The habitat consists of long slopes (300–500 m) with slopes of 10–15 %. Vegetation canopy cover varies (20–45 %), while rock cover ranges between 35 % and 80 %. Large dolerite boulders provide a more diverse habitat, with a higher vegetation canopy cover compared to the steeper shale slopes. The average number of species found per relevé is 14.

The *Tylecodon wallichii - Euphorbia hamata* Succulent Dwarf Shrubland is characterised by Species Group B (Table I), with the diagnostic species *Tylecodon wallichii*, *Lampranthus diffusus* and *Pteronia villosa*. Other common species are *Euphorbia hamata*, *Euphorbia decussata*, *Pteronia pallens*, *Felicia lasiocarpa*, *Eriocephalus spinescens* and *Augea capensis*. *Pteronia intermedia*, *Tetragonia fruticosa* and *Tripteris sinuata* are also abundant in localised areas. Swarms of bees were active in these hills and an Africa wild cat, *Felis lybica*, was flushed out of a rocky drainage line.

1.2 The *Monechma spartioides - Tripteris sinuata* Dwarf Shrubland of the more south facing steep slopes (Fig. 4):

These south-facing hill slopes between 518 m and 580 m a.s.l., consist of rocky shale scree slopes strewn with dolerite rocks in localised areas. Vegetation canopy cover varies (5–25 %), and rock cover varies between 35 % and 80 %. Average number of species found per relevé is 16.

The *Monechma spartioides - Tripteris sinuata* Dwarf Shrubland community is characterised by Species Group C, with diagnostic species such as *Monechma spartioides*, the most dominant, *Sericocoma avolans, Pteronia mucronata, Asparagus capensis* and *Hermannia spinosa* (Table I). Other common species are *Zygophyllum microcarpum, Aridaria noctiflora, Eriocephalus spinescens* and *Ruschia spinosa*, with *Tripteris sinuata*, *Galenia africana* and *Enneapogon scaber* particularly abundant.

1.3 The *Euphorbia hamata - Ruschia spinosa* Dwarf Shrubland on the dolerite/shale, rocky hilltops (Fig. 4):

This community is generally diverse with a concave rocky or convex shallow sandy surface. Vegetation canopy cover varies between 3 % and 30 % with rock cover varying between 50 % and 90%. Average number of species found per relevé is 13.

The *Euphorbia hamata - Ruschia spinosa* Dwarf Shrubland is characterised by the absence of Species Groups B and C, and the presence of Species Group A, which is also common to the former two hill communities (Table I). Shrubs are higher in the more sandy convex areas, with species such as *Pteronia pallens, Berkheya spinosa, Tripteris sinuata* and *Pteronia viscosa*. In the more rocky areas species such as *Euphorbia hamata, E. decussata, Ruschia spinosa* and *Zygophyllum microcarpum* occur. Many other species, rare and absent in the other communities are also found including *Lycium bosciifolium, Limeum aethiopicum, Oncosiphon pilulifera, Ruschia* sp. cf. *R. karrooica* and *Drosanthemum hispidum*.

2. The *Stipagrostis ciliata - Salsola aphylla* Grassland of the dolerite plateau (Fig. 5b):

These elevated dolerite plateau's occur in the central western section of the park at 396–427 m a.s.l. (Fig. 4). The topography is slightly undulating but predominantly convex with low shale mounds protruding through the dolerite. On the edge of this plateau, a severely eroded layer of dolerite protrudes, consisting of a thin, flat layer eroding into small round stones on top. No large dolerite boulders are present on the central plateau, as is typical with most dolerite hills and dykes, although two rocky dolerite dykes surveyed also fell into this community. The steep slopes below the dolerite cap of this plateau consist of almost white soft shales. The centre of the plateau is convex with no stones, and deeper red sandy soils.

The land type for this area is R1 (Land Type Survey Staff 1996), with Hutton soils consisting of a structureless orthic A horizon, which at the depth of 40–50 mm change to a single particled to massively structured red B horizon with underlying rock at a depth of 150–500 mm. Soil analyses (Table 2) showed these soils to be fairly alkaline ($pH_{(KCl)}$ 7.9–8.2), with low phosphates (2–5 mg/kg), and much lower sodium contents than the rest of the park (28–90 mg/kg). Soil texture is very sandy with low clay and silt contents. Vegetation canopy cover varies (10–25 %), vegetation appears homogeneous with a low species diversity, and the average number of species found per relevé is 9.

The *Stipagrostis ciliata - Salsola aphylla* Grassland is characterised by Species Group D (Table 1) with the abundance of the grass *Stipagrostis ciliata* making this community appear lush compared to the rest of the park. Other diagnostic species that occur in localised areas are *Salsola cryptoptera*, *Babiana truncata* (visible only after good rains), *Lebeckia spinescens, Melolobium exudans, Salsola zeyheri* and the occasional *Stipagrostis namaquensis* clumps. Plants such as *Salsola aphylla, Aridaria noctiflora, Eriocephalus spinescens*, and the grass *Stipagrostis obtusa* are also common.

3. The *Ruschia wittebergensis - Salsola aphylla* Dwarf Shrubland of the limestone lenses (Fig. 5c):

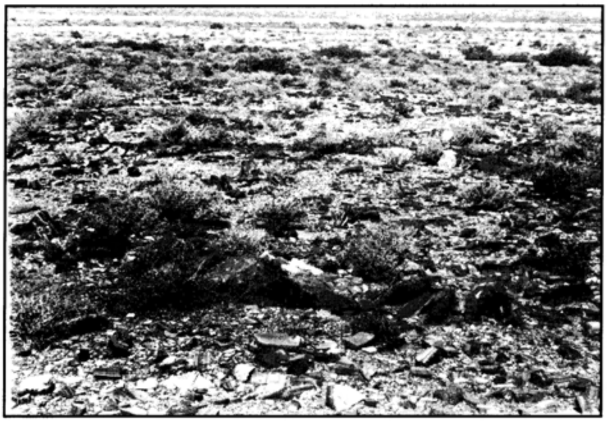
The limestone outcrops are found in the central section of the park, at 366 m a.s.l., in localised areas below the dolerite plateau of community 2 (Fig. 4). Terrain form is broken to flat with large dark grey limestone rocks, weathered into sharp grooves with an elephant skin texture on the one side, and smooth shiny black manganese secretions on the other. White calcrete layers and quartz are also visible in localised areas. Soil samples (Table 2) indicated a high $pH_{(KCl)}$ (7.7–8.2), with low phosphates (3–6 mg/kg) and high Ca (2850–22170 mg/kg), K (134–264 mg/kg), Mg (231–287 mg/kg) and Na (175–305 mg/kg) contents.

This community falls into land type Ms2 (Land type Survey Staff 1996). The soil texture varies between sandy clay and sandy clay loam, with clay contents between 18 % and 67 %. The Mispah soil forms consist of

Fig. 5. Examples of some of the major plant communities (a-k) of the Tankwa-Karoo National Park.

a. The *Euphorbia hamata – Pteronia pallens* Dwarf Shrublands of the prominent hills.

b. The *Stipagrostis ciliata* - *Salsola aphylla* Grassland of the dolerite plateau.



c. The *Ruschia wittebergensis* - *Salsola aphylla* Dwarf Shrubland of the limestone lenses.

d. The *Salsola aphylla* - *Lycium cinereum* Shrubland of the more silty drainage lines and floodplains.

weekly structured orthic A horizons that change to hardpan calcrete. This hardpan calcrete is described by MacVicar *et al.* (1977) as a superficial limestone formed by the cementation of soil, sand or gravel by calcium carbonate. The lower part of calcrete is often soft and porous while the upper layers are hard. Vegetation canopy cover is low (5 %) and rock cover is high (75 %) in this community. The average number of plant species found per relevé is 14.

The *Ruschia wittebergensis* - *Salsola aphylla* Dwarf Shrubland is characterised by Species Group E (Table I) with diagnostic species such as *Ruschia wittebergensis, Bulbine alooides, Pteronia glabrata, P. lucilioides, Gnidia polycephala, Jamesbrittenia atropurpurea* and *Berkheya spinosa*. Other common species are *Salsola aphylla, Lotononis densa, Zygophyllum microcarpum* and *Aridaria noctiflora*, with *Salsola* and *Zygophyllum* species more common on the lower lying soft, porous calcrete.

4. The *Lycium cinereum* - *Malephora luteola* plain communities

The plains of the TKRNP cover the largest area of the park and consist of Dwyka and Ecca shales at 335–396 m a.s.l. The plains communities are common for land types M2 (Community 4.1) and M3 (Communities 4.2 & 4.3) (Land Type Survey Staff 1996), with plains consisting of 45 % of land type M2 and 85 % of land type M3.

The topography varies from flat to slightly concave gravel areas to convex sandy areas to drainage lines and floodplains. Gravel varies between fine gravel, courser gravel to various textures and colours of desert paving mudstone and siltstone. The thin layers of desert paving on top of deeper layers of soil are sensitive to disturbance by vehicles, with disturbances probably resulting in wind and sheet erosion removing the soil up to the next protective layer of desert paving.

In the drainage lines and floodplains, higher plant species diversity, vegetation cover, and animal activities are found. Species Group F is diagnostic for the plains with species of Species Groups I and F (Table 1) common in the drainage lines and flood plains.

4.1 The *Salsola aphylla - Lycium cinereum* Shrubland of the more silty drainage lines and floodplains (Fig. 4 & 5d):

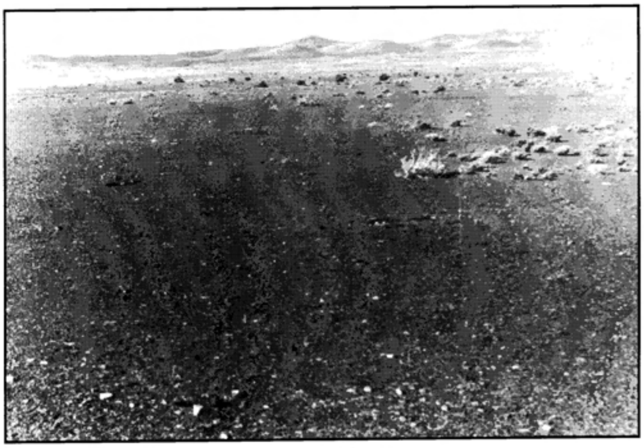
Soil analyses indicated alkaline, sodic soils with $pH_{(KCl)}$ between 7.8 and 8.3 (Table 2). Soil texture is sandy loam to sand-clay-loam. Drainage lines vary from well established shrub communities (Species Group G) along the banks and surrounding floodplains (vegetation canopy cover 55 %), to generally more sparse drainage lines where water drains faster due to a slight gradient (cover 2-5 %). The average number of plant species found per relevé is 10, yet these drainage lines contribute most to the diversity of the *Lycium cinereum - Malephora luteola* plain communities (Table 4a).

The diagnostic species along the banks of the drainage lines are characterised by Species Group G, with *Eriocephalus capitellatus* one of the more prominent characteristic shrubs (Table 1). Common species on these floodplains are *Salsola aphylla, Tripteris oppositifolium, Lycium cinereum, Malephora luteola, Aridaria noctiflora, Zygophyllum microcarpum* and *Augea capensis*. More rare species such as *Othonna pteronioides* are also found in localised areas along the drainage lines.

4.2 The *Cladoraphis spinosa - Lycium cinereum* sandy floodplain community (Fig. 4):

Vegetation canopy cover is generally very even (10-15 %) while the soils are sandier with gravel. This community is characterised by Species Group H, with the diagnostic species *Cladoraphis spinosa, Salsola contrariifolia, Ornithogalum xanthoclorum,* and *Lotononis pungens* (Table 1). Common species are similar to those in community 4.1, while the most common prominent species are *Cladoraphis spinosa* and *Malephora luteola*. The average number of plant species found per relevé is 15.

Drainage lines generally have more shelter, food or nesting material for numerous species of insects, birds or mammals (Milton 1990).



e. The *Zygophyllum microcarpum - Lycium cinereum* Open Plains.

4.3 The *Zygophyllum microcarpum - Lycium cinereum* Open Plains (Figs. 4 & 5e):

This community is the largest plant community in the park found on the Ecca shales. Vegetation canopy cover is low (2–4 %) and the soil surface is generally flat and covered with shale gravel and/or sand. Soil forms consist predominantly of Mispah (55 %) and Glenrosa (20 %) (Land Type Survey Staff 1996). The $pH_{(KCl)}$ of the soil sample for this area is 7,6, with the sodium and silt contents lower than in the flood plains (Table 2). The average number of plant species found per relevé is 9, with species diversity contributed by succulents being particularly low (Table 4c).

The *Zygophyllum microcarpum - Lycium cinereum* open plains community is distinguished from communities 4.2 and 4.1 by the absence of Species Groups G, H and I (Table I). The common species include Species Groups F, M and Q with the most prominent species consisting of *Augea capensis* and *Stipagrostis obtusa*. Annuals that are common in this community include *Euryops annuus, Ursinia nana* and probably other species, that were not recorded as the surveys were done during a very dry period. During a seedbank study done in this plant community, some of the seedlings were identified as: Mesembryanthemaceae, grass species, *Tetragonia microptera, Ursinia nana, Foveolina albida, Troglophyton parvulum, Amellus tridactylus* subsp. *arenarius, Euryops annuus*, and some large grass species.

5. The *Ruschia spinosa - Ruschia* cf. *robusta* Succulent Dwarf Shrubland (Fig. 4):

These communities commonly occur on the more elevated areas, where the soils are generally shallow and stony. Species Group J is characteristic of all the plant communities that occur in the *Ruschia spinosa - Ruschia* cf. *robusta* Succulent Dwarf Shrubland, with the succulents *Ruschia spinosa, Rushcia robusta* and *Drosanthemum eburneum* and the dwarf shrub *Galenia fruticosa* some of the most common species.

5.1 The *Drosanthemum delicatulum - Ruschia spinosa* Dwarf Shrubland of the rocky drainage lines.

The drainage lines cross a diverse environment, with vegetation canopy cover generally between 10 % and 15 %, and rockiness varying between 10 % and 90 %, consisting of shale rocks or gravel. The average number of species found per relevé is 16. The analysis of one soil sample collected on the edge of a rocky drainage line indicated a low $pH_{(KCl)}$ of 4.2 and also low calcium content (94 mg/kg) (Table 2).

The *Drosanthemum delicatulum - Ruschia spinosa* Dwarf Shrubland is characterised by Species Group K, with some of the prominent diagnostic species *Aridaria* sp., *Psilocaulon utile, Pteronia punctata, Cephalophyllum ebracteatum, Drosanthemum delicatulum, D. lique* and *D. cymiferum* (Table 1). The *Drosanthemum* species are very closely related and may in future be lumped as one species (C. Bredenkamp, National Botanical Institute, Pretoria. *pers. comm.*). Other common species are *Aridaria noctiflora, Zygophyllum microcarpum, Augea capensis, Ruschia spinosa, Ruschia* cf. *robusta, Galenia fruticosa, Drosanthemum eburneum, Tripteris sinuata* and *Galenia africana*.

The vegetation of the drainage lines in these rocky broken areas is diverse and biodiversity is higher than the rest of the *Ruschia spinosa - Ruschia* cf. *robusta* Succulent Dwarf Shrubland communities (Table 4a). Species common in the floodplains and plains of the former communities (Species Groups L & M) were also found in these drainage lines. The effect of drainage on vegetation pattern has been noted in arid environments worldwide (Leistner 1967; Noy-Meir 1985; Werger 1985; Stafford-Smith & Morton 1990 *In*: Milton 1990). In deserts species richness increases in depressions and runnels receiving run-off water and plant life-form diversity tends to be higher (Milton 1990).

5.2 The *Rhinephyllum macradenium - Ruschia spinosa* Succulent Dwarf Shrubland of the low lying Dwyka shale desert paving.

The community occurs in the plains of land type Ms2, and the dominant soil forms are Mispah (20 %), Hutton (40 %) and Glenrosa (10 %) (Land Type Survey Staff 1996).

Habitat of this community is predominantly flat, to slightly undulating and occurs at 365 m a.s.l. Vegetation canopy cover varies (0–15-30 %). The average number of species found per relevé is 17. Ground cover consists of a thin layer of grey black to shiny black desert paving gravel.

This community has large areas denuded of any vegetation except for localised patches of flat growing mesemb species growing in dense crusts, normally adjacent to dense stands of *Ruschia spinosa* and *Ruschia* cf. *robusta.* In early spring during good rainfall years a colourful display of annuals appears in the bare areas. A higher species diversity is found where deeper, less compacted alluvial gravel soils have accumulated with species such as *Salsola rabiena* and *Bassia salsoloides* also present.

The *Rhinephyllum macradenium - Ruschia spinosa* Succulent Dwarf Shrubland is characterised by Species Group N, with diagnostic species *Rhinephyllum macradenium, Bulbine species, Tripteris clandestina, Heliophila deserticola*, and endemics such as *Tanquana prismatica* (rare) and *Eurystigma clavata*. Other common perennial plants that occur in this community, are *Augea capensis, Ruschia spinosa, Ruschia* cf. *robusta, Galenia fruticosa* and *Drosanthemum eburneum*. *Malephora luteola* is common in localised areas, *Crassula muscosa*, in low densities, and only one occurrence of *Anthospermum dregei* was found, in a shallow drainage line.

5.3 The *Cheiridopsis acuminata - Ruschia spinosa* Dwarf Shrubland (Fig. 4).

Although this survey identified only one community, visually this mesemb community can be separated into discrete units due to topography, the distribution of the vegetation, and stone or gravel surface cover. These communities occur on: (i) the more even sloped Dwyka tillites (Fig. 5f); (ii) the larger red Dwyka shale hills (Fig. 5g); (iii) the sharply undulating black desert paving areas with topography influenced by many dry drainage lines; and (iv) a narrow gently sloped homogeneous area (Fig. 5h), paved with red-black sandstone stones (3–5 cm in diameter) (Fig. 4).

f. The *Cheiridopsis acuminata - Ruschia spinosa* Dwarf Shrubland on the the more even sloped Dwyka tillites.

g. The *Cheiridopsis acuminata - Ruschia spinosa* Dwarf Shrubland on the larger red Dwyka shale hills.

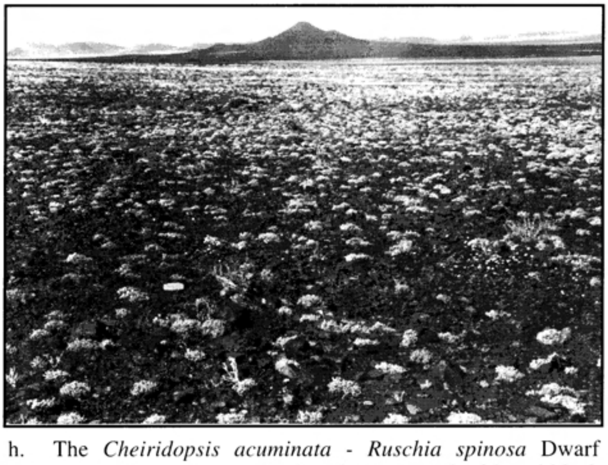
The *Cheiridopsis acuminata - Ruschia spinosa* Dwarf Shrublands occur on the slopes and crest of hills in land type Ms2 and Ms3 (Land Type Survey Staff 1996) at 365–427 m a.s.l. Soil forms are generally 35–50 % Mispah, 15–30 % Glenrosa and 25–30 % rock. Soil sample analyses indicated a variable pH, with high Ca content. Soils on the termitaria (found only on the Dwyka tillites and in community 5.4 on the more elevated Ecca shales) are more alkaline ($pH_{(KCl)}$ 8.3), with high Ca (2780 mg/kg) and Na (885 mg/kg) content (Table 2). As soil salinity, conductivity and nitrogen status decrease towards drainage lines, there is a concomitant reduction in the cover of succulent species (Milton 1990). The average number of species found per relevé is 10.

The *Cheiridopsis acuminata - Ruschia spinosa* Dwarf Shrubland community is characterised by Species Group P and the absence of Species Groups K to O (Table 1), which are more common in the lower lying areas of community 5. The diagnostic species include *Cheiridopsis acuminata, Mesembryanthemum* cf. *nodiflorum, M. stenandrum* and *Hereroa fimbriata*. Some of the diagnostic annuals are *Osteospermum pinnatum* var. *pinnatum, Heliophila digitata, Nemesia ligula* and *Hebenstretia parviflora*. Common species of Species Group Q, generally common on the rocky or sandy plains, are also absent from this community. Other species that occur in high densities are *Ruschia spinosa, Ruschia* cf. *robusta* and the annuals of Species Group R. Common but less abundant species include *Galenia fruticosa, Drosanthemum eburneum* and *Pteronia intermedia*.

The topography of the Dwyka tillite section of this community is fairly even and gradually slopes in a south-easterly direction. Vegetation cover on the Dwyka tillites is also more evenly distributed (vegetation canopy cover 15–20%), with regularly spaced bare termitaria patches. These termitaria or heuweltjies generally support taller, denser vegetation with a higher woody or succulent component than the surrounding areas. This pattern is reversed in the park. Milton *et al.* (1997) describes this pattern for overgrazed areas and on shallow soils where they tend to be barer than their surroundings and dominated by annuals such as *Euryops annuus*.

The sharply undulating black desert pavement communities only have vegetation in localised areas, with large areas denuded of vegetation, but covered in a monoculture of annual mesembs, resembling green lawns during spring in good rainfall years. Most of these annual mesembs have not been identified as they only started blooming late in October after most of the other annuals had finished flowering.

The even sloped sandstone paved area has a homogeneous spread of vegetation dominated by *Drosanthemum eburneum* (relevés 55-57, Table I), with the conspicuous absence of *Ruschia spinosa, Ruschia* cf. *robusta* and *Galenia fruticosa* (Species Group J).



h. The *Cheiridopsis acuminata - Ruschia spinosa* Dwarf Shrubland on a narrow even sloped area paved with red-black sandstone stones.

5.4 The *Tripteris sinuata - Ruschia spinosa* Dwarf Shrubland of the upper slopes of the elongated Ecca plains (Fig. 4).

This community falls only into land type Ms3 at 427 to 518 m

Table 4

Species richness and species evenness indices computed for the major plant communities of the Tankwa-Karoo National Park

(a.) All species:

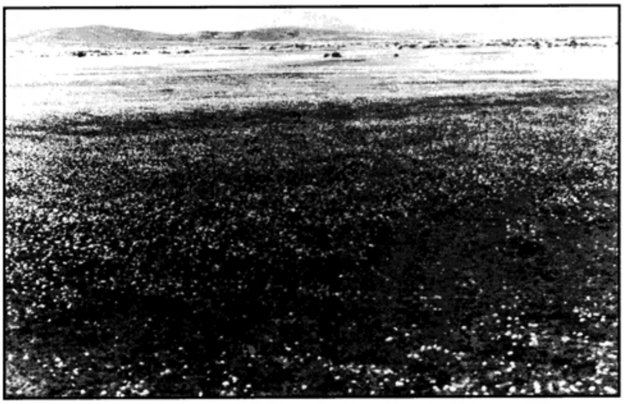
Community	Shannon	Berger-P	Margaleff	S	% Cover	Number of relevès
1.1	3.36	6.52	20.79	51.0	11.1	5
1.2	3.37	5.41	23.59	64.0	14.5	7
1.3	2.50	2.41	10.96	35.0	22.3	4
1	3.79	6.64	39.54	109.0	15.4	16
2	3.13	5.67	15.24	33.0	8.2	5
3	2.71	3.15	15.28	47.0	20.3	7
4.1	3.32	5.91	24.92	55.0	8.7	9
4.2	2.99	8.46	11.77	35.0	18.0	4
4.3	2.21	2.94	11.45	25.0	8.1	10
4	3.40	7.22	32.46	76.0	10.1	23
5.1	3.16	7.77	16.31	47.0	16.8	7
5.2	3.04	5.71	14.97	52.0	30.2	7
5.3	2.80	5.35	19.61	52.0	13.5	13
5.4	2.63	5.37	13.52	40.0	17.9	6
5	3.46	6.32	36.66	108.0	18.5	33
6	2.94	7.52	13.06	42.0	23.1	7
7	2.20	3.19	11.69	24.0	7.2	7

(b.) Only perennial and succulent plants:

Community	Shannon	Berger-P	Margaleff	S	% Cover	Number of relevès
1.1	3.07	4.39	16.92	35.0	7.5	5
1.2	3.10	4.84	18.75	49.0	12.9	7
1.3	2.27	2.24	8.57	27.0	20.8	4
1	3.47	5.70	30.25	79.0	13.2	16
2	2.91	5.00	12.66	26.0	7.2	5
3	2.47	2.95	10.87	33.0	19.0	7
4.1	2.98	5.16	18.22	38.0	7.6	9
4.2	2.67	7.24	9.15	26.0	15.4	4
4.3	2.01	2.71	9.42	20.0	7.5	10
4	3.10	6.39	23.30	52.0	8.9	23
5.1	3.02	7.42	13.71	39.0	16.0	7
5.2	2.48	4.17	9.70	31.0	22.0	7
5.3	1.93	3.09	14.64	31.0	7.8	13
5.4	2.17	3.68	8.83	23.0	12.1	6
5	2.95	4.54	26.26	69.0	13.3	33
6	2.38	4.87	8.51	24.0	14.9	7
7	2.08	6.33	-13.10	9.0	0.5	7

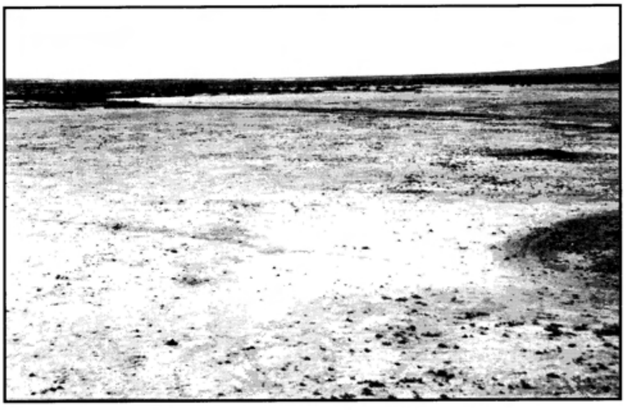
(c.) Only succulent plants:

Community	Shannon	Berger-P	Margaleff	S	% Cover	Number of relevès
1.1	2.16	4.37	10.54	12.0	2.8	5
1.2	1.96	3.67	15.77	11.0	1.9	7
1.3	1.19	1.43	4.26	12.0	13.3	4
1	2.13	2.17	14.87	25.0	5.0	16
2	1.55	2.38	8.66	7.0	2.0	5
3	0.66	1.20	12.66	5.0	1.4	7
4.1	1.99	3.27	12.85	11.0	2.2	9
4.2	2.00	3.92	9.36	9.0	2.4	4
4.3	0.59	1.20	3.33	5.0	3.3	10
4	1.64	1.94	14.05	15.0	2.7	23
5.1	2.43	5.15	7.89	20.0	11.1	7
5.2	1.91	2.98	5.08	15.0	15.8	7
5.3	1.63	2.85	9.64	20.0	7.2	13
5.4	1.34	2.37	3.41	8.0	7.8	6
5	2.31	3.39	14.37	34.0	9.9	33
6	1.34	2.30	2.77	6.0	6.1	7
7	1.31	3.33	-2.39	4.0	0.3	7



i. The denuded to bare areas on shale hills covered in spring by a spectacular display of monoculture stands of annual species such as *Gazania lichtensteinii*.

j. The denuded to bare areas on desert paved gravel covered in spring by unidentified annual *Mesembryanthemum* species.



k. The alluvial floors.

a.s.l. Topography is uniform with a gradual slope and regular erosion rills fanning out in a southern and south-western direction. Dominant soil forms are Mispah and Glenrosa and slope is 1–3 % (Land Type Survey Staff 1996). Soil analyses indicated that $pH_{(KCl)}$ varied between 5.8 and 7.9, with the regularly scattered bare termitaria patches having soils that are more leached (pH 5.8), with high phosphate contents (Table 2). Soil texture is described as a sandy clay-loam. Vegetation canopy cover varies (5–25 %), rockiness between 55–70 %, and the average number of species found per relevé is 12.

The *Tripteris sinuata - Ruschia spinosa* Dwarf Shrubland is characterised by the absence of diagnostic species from Species Groups K, L, M, N, O and P (Table I), that occur in the rest of the *Ruschia spinosa - Ruschia* cf. *robusta* Succulent Dwarf Shrubland communities. The most dominant species are *Ruschia spinosa*, and to a lesser extent *Ruschia* cf. *robusta,* with *Euphorbia restituta* prominent but sparsely scattered. Species such as *Tripteris sinuata*, *Stipagrostis obtusa* and *Galenia africana* indicate the plains character of this community, with *Galenia africana* particularly abundant in the erosion rills. The annuals *Euryops annuus, Gazania lichtensteinii* and to a lesser extent *Ursinia* and *Arctotis* species are common on the otherwise denuded termitaria.

6. *The Brownanthus ciliatus - Enneapogon scaber Dwarf* Shrubland of the Kimberlite hills (Fig. 4).

The Kimberlite hills are conspicuous mound shaped hills, with a height of 20–45 m. They occur in land type Ms3 (Land Type Survey Staff 1996) at 365–413 m a.s.l. Vegetation canopy cover on these hills varies from 8 % to 15 %, and the average number of species found per relevé is 14. The shale and sandstone rock cover is high (80-90 %). Only the sparsely scattered annual, *Euryops annuus*, grows on the top of these hills during spring.

The *Brownanthus ciliatus - Enneapogon scaber* Dwarf Shrubland of the Kimberlite hills are characterised by the absence of any diagnostic species. The abundance of *Brownanthus ciliatus, Enneapogon scaber* and *Galenia crystallina* from Species Group Q, and the absence of any of the former species groups are characteristic of these hills. Species diversity increases dramatically on the cooler southern slopes, with some of the most common species on these hills being *Tripteris sinuata*, *Stipagrostis obtusa*, *Atriplex lindleyi* subsp. *inflata* and *Amellus tridactylus* subsp. *arenarius* (Species Group Q), and less common annuals (Species Group R). The cooler southern slopes also have prominent species such as the succulent *Tylecodon wallichii* and the shrub *Rhus undulata* (rare).

7. The denuded to bare areas on desert paved gravel and shale hills

Throughout the park large denuded areas occur, particularly in communities 4.3 (Ecca shale plains), 5.2 (flat low-lying Dwyka shale desert paving) and 5.3 (iii) (the sharp undulating Dwyka shales). During good winter and spring rainfall years, these areas are covered in spring by a spectacular display of almost monoculture stands of annual species such as *Gazania lichtensteinii* (Fig. **5i**), *Osteospermum pinnatum* var. *pinnatum*, *Euryops annuus, Ursinia nana, Oncosiphon grandiflorum* (Species Group R) and unidentified *Mesembryanthemum* species (Fig. **5j**) (Table 1).

8. Alluvial floors (Fig. 4 & 5k).

The alluvial floors are generally denuded of any vegetation, and no vegetation surveys were done on them during this study period. After good rains, these floors are rapidly covered by succulent forbs, which is a plant life form characteristic of saline soils (Milton 1990). Sand driven along close to the ground frequently accumulates about Salsola bushes, which produce the typical elevated shrub clumps that occur around the edge of an alluvial floor. The Oakleaf soils that occur on these floors and pans are high in silt, often with more silt than clay. Because of the flatness of this area, pans tend to form. Surface water flows easily and the area is susceptible to erosion (Land Type Survey Staff 1996).

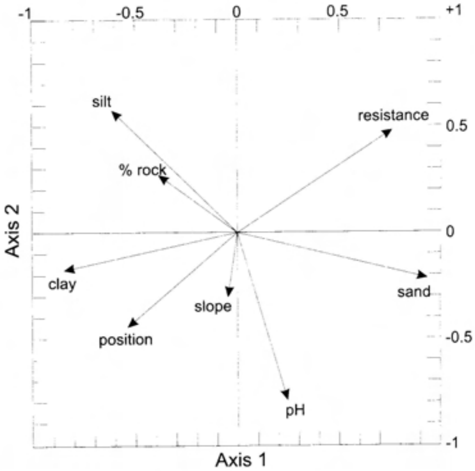


Fig. 6. The eigenvector loadings on the first two axes of a correlation-type principal components analysis of eight topo-edaphic variables (eigenvalues: axis 1=0.42, axis 2=0.22; 64% of the variance). Percentage rock was made passive. Variables are positively correlated if their arrows subtend a small angle, orthogonal if their arrows are at 90°, and negatively correlated if their arrows are in opposite directions.

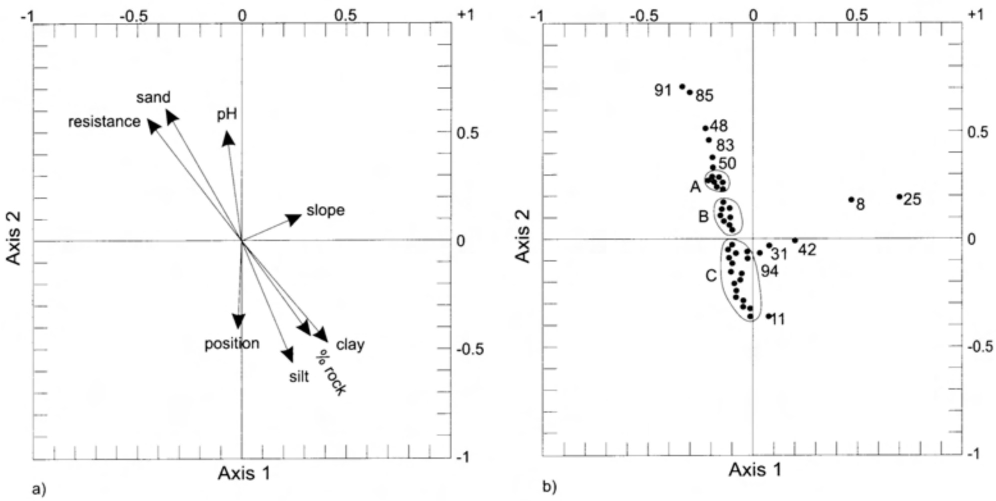


Fig. 7. Plots of the first two axes of the correspondence analysis of 30 samples (two passive): a) environmental variables, and b) species. Refer to Table 3 for how well the ordinations performed. Environmental variables with the longest arrow relative to an axis have the greatest influence on that axis. If the arrows of two variables subtend a small angle they are correlated: if they subtend an angle of 90 they are orthogonal; if they subtend an angle of >90 they are negatively correlated. The order of species along any environmental variable is obtained by dropping a perpendicular bisector from the species to the extended line of the arrow. Key to the species: 1 - *Aptosimum indivisum*, 3 - *Aridaria noctiflora*, 4 - *Aridaria* sp., 5 - *Atriplex lindleyi* ssp. *inflata*, 6 - *Augea capensis*, 8 - *Bulbine alooides*, 11 - *Cephalophyllum ebracteatum*, 12 - *Cheiridopsis acuminata*, 14 - *Crassula deltoidea*, 15 - *C. muscosa*, 16 - *C. subaphylla*, 17 - *Crotalaria* sp., 21 - *Drosanthemum eburneum*, 25 - *D. wittebergensis*, 28 - *Eriocephalus spinescens*, 29 - *Euphorbia decussata*, 31 - *E. restituta*, 34 - *Galenia africana*, 35 - *G. fruticosa*, 36 - *Gazania lichtensteinii*, 37 - *Gnidia polycephala*, 38 - *Hereroa fimbriata*, 42 - *Lachenalia mutabilis*, 44 - *Lapeirousia pyramidalis*, 48 - *Lotononis densa*, 49 - *Lycium cinereum*, 50 - *L. ferocissimum*, 52 - *Malephora luteola*, 53 - *Mesembryanthemum* sp., 55 - *Moraea speciosa*, 58 - *Osteospermum pinnatum*, 61 - *Oxalis* spp., 65 - *Psilocaulon absimilae*, 68 - *P. utile*, 69 - *Pteronia glabrata*, 70 - *P. lucilioides*, 73 - *P. pallens*, 76 - *P. villosa*, 79 - *Ruschia robusta*, 80 - *R. spinosa*, 82 - *R. wittebergensis*, 83 - *Salsola aphylla*, 85 - *S. cryptoptera*, 87 - *S. nigrescens*, 89 - *Sarcocaulon crassicaule*, 91 - *Stipagrostis ciliata*, 93 - *S. obtusa*, 94 - *Tetragonia echinata*, 95 - *T. fruticosa*, 98 - *Tripteris sinuata*, 101 - *Zygophyllum microcarpum*. To avoid congestion, the following species groups are given in b) listed as they occur in the graph from top to bottom A = 17, 69, 73, 1, 37, 71; B = 82, 28, 65, 5, 9, 3, 87, 76, 6, 61, 101, 71, 52, 55, 37; and C = 49, 44, 99, 53, 35, 34, 36, 68, 4, 89, 29. 95, 80, 70, 14, 98, 15, 12, 38.

Vegetation-environmental gradients

In a PCA containing all the environmental and soil data, each axis accounted for approximately 20 % of the variance. This indicates that many different topo-edaphic factors played a role. In the PCA where only the variables $pH_{(KCl)}$, resistance (Ohm), percentage sand, silt, clay, percentage slope, catenal position and percentage rock were used, the first two axes accounted for 64 % of the variance, showing an obvious textural gradient (Fig. 6). Sandy areas, such as the dolerite plateaus, had a low conductance (high resistance, Ohm), and were negatively correlated to the lower-lying shale plains (catenal position), which had a high percentage silt and clay in the soils (Fig. 6).

In the PCA done only on the mineral content and catenal position, 50 % of the variance were accounted for by the first two axes.

Most of the minerals, copper, manganese, zinc, magnesium and phosphate rich soils were found in the low-lying areas. These soils were negatively correlated with calsium rich soils which were common in the limestone outcrops and surrounding areas. On the second axis both phosphate and magnesium were negatively correlated to all the other minerals.

The CA and CCA ordinations were not fundamentally different in their performance, particularly for the first axis. The species variance accounted for by the first four axes of the CA was not excessively greater than the species variance accounted for by CCA, while the variance of the species-environment relation accounted for by CCA was approximately 1.4 times higher than that accounted for by CA (Table 3). This indicates that most important environmental factors were accounted for. The overall ordination and first axis of the CCA were also significant ($P < 0.01$), confirming that the measured topo-edaphic variation explained a significant proportion of community variation. The variables accounting for the variance on the first axis were similar for the CA and the CCA (Table 3), but not for the subsequent axes. The differences between the axes in their eigenvalues for all 8 axes of the CA are fairly small, indicating that the pattern of floristic variation is due to a composite of smaller, almost equivalent, independent gradients. In all the CA axes the environmental gradient seem to have a fairly similar effect on species distribution. Figure 7 depicts this gradient with slopes of shale hills typically with species such as *Drosanthemum wittebergense, D. eburneum* and *Brownanthus ciliatus*, while axis 2 shows the most pronounced gradient. The sandy, high resistance soils typical of the dolerite plateau showed an association with species such as *Stipagrostis ciliata, Salsola cryptoptera, Lotononis densa, Salsola aphylla* and *Lycium ferocissimum*. A negative correlation was found with the more clay and silt rich soils, associated with typical mesemb species such as *Hereroa fimbriata, Cephalophyllum ebracteatum* and *Cheiridopsis acuminata*.

Discussion

Herbivory by domestic livestock has probably altered species composition of large sections of the park. This is common to most of the succulent Karoo (Milton *et al.* 1997), where perennial species, which are lost through grazing mismanagement, do not re-establish within a few decades. Perennial species lack dormant seeds, have short dispersal distances, or are excluded by competition with other perennials, which have filled the spaces left by their demise. There thus appears to be no rapid, reliable or economically feasible method for restoring function and species diversity to such rangelands (Milton *et al.* 1997).

Exotic species that pose a threat to large sections of arid land in South Africa also occur in the park. *Prosopis glandulosa*, a tree used for sheep and goat fodder, was actively cultivated around the homestead of Varsfontein, and a few specimens have been planted at the historical homesteads of Luiperdskop and Volmoesfontein. This tree is gradually spreading and a number of seedlings occur around all the homesteads, and in most drainage lines. No thickets of *Prosopis glandulosa* are present inside the park, but dramatic infestations are visible along the banks of the Tanqua River, outside the southern boundary of the park. *Nicotiana glauca* seedlings are also present in the park, with huge infestations found in the Renoster River and adjacent flood plains due east of the park. Other exotic species found in the park are the grasses *Bromus rigidus* and *Lophochloa pumila* and the common tumbleweed *Salsola kali*. Neither of these species occurred in high densities, while the small shrub *Atriplex lindleyi* subsp. *inflata* from Australia, is a major alien invasive in the park.

Areas of highest plant species diversity were identified with this study. The succulent component dominates in communities 1 (1.1, 1.2 & 1.3) and 5 (5.1, 5.2, 5.3, & 5.4), which comprises approximately 40 % of the park. The highest species richness also occurs within these communities (Table 4), which

Table 5

Plant species identified in the Tankwa-Karoo National Park

Middle column
plant guilds as in Milton *et al.* (1997): E = annuals; EV = annual succulents; BD = Geophytes Dicotyledons; BM = Geophytes Monocotyledons; G = Graminoid; L = Lianes & Vines; SD = Dwarf shrubs (< 60 cm high); SM = Mid-high shrubs (60-200 cm); VG = contracted, stemless, all leaves at ground level; VM = succulent perennial shrubs; VMS = stem succulents; ? = uncertain; # = endemic to Tanqua Karoo and immediate adjacent areas of Sutherland and Roggeveld plateau (J. Vlok)
$ = endemic to Tanqua Karoo (C. Hilton-Taylor)
Last column:
B = Identification done by Bruce Bayer - 23-25 September 1992
V = Identification done by Jan Vlok - 9 September - 9 October 1996; N = Identification done by the National Botanical Institute; Numbers = refers to personal collecting record numbers of F. Rubin

	Guilds	Identification
JUNCACEAE		
Juncus L.		
J. acutus L. B		
subsp. *leopoldii* (Parl.) Snog.	G	
COLCHICACEAE		
Androcymbium Willd.		
A. capense (L.) Krause	BM	V 309
A. pulchrum Schltr. & Krause	BM	V 178
Ornithoglossum Salisb.		
O. viride (L. f.) Ait.	BM	V 242
POACEAE		
Merxmuellera Conert		
M. dura (Stapf) Conert	G	B
Karroochloa Conert & Tuerpe		
K. tenella (Nees) Conert & Tuerpe	G	B
Stipagrostis Nees		
S. brevifolia (Nees) De Winter	G	B
S. ciliata (Desf.) De Winter		
var. *capensis*	G	N 3922
(Trin. & Rupr.) De Winter		
S. namaquensis (Nees) De Winter	G	
S. obtusa (Del.) Nees	G	V 180, 223
Cladoraphis Franch		
C. spinosa (L. f.) Toelken	G	N 3889
Enneapogon Desv. ex Beauv.		
E. scaber Lehm. var. *scaber*	G	N 16, 62, V 238
Fingerhuthia Nees		
F. africana Lehm.	G	V 307
Lophochloa Reichenb.		
**L. pumila* (Desf.) Bor	G	N 125
Bromus L.		
B. pectinatus Thunb.		V 296
**B. rigidus* Roth	G	N 3937
ASPHODELACEAE		
Bulbine Willd.		
B. alooides (L.) Willd.	VG	V 143, 59
Haworthia Duval		
Haworthia sp.	VG	V (*pers. obs.*)
Trachyandra Kunth		
T. oligotricha (Bak.) Oberm.	BM	V 162
Chlorophytum Ker-Gawl.		
C. undulatum (Jacq.) Oberm.	BM	V 144
HYACINTHACEAE		
Albuca L.		
A. maxima Burm. f.	BM	V 271
A. cooperi Bak.	BM	V 282
A. spiralis L.f.	BM	V
Albuca sp.	BM	*pers. obs.*
Dipcadi Medik.		
D. brevifolium (Thunb.) Fourc.	BM	V 258
D. crispum Bak.	BM	N 40
Ornithogalum L.		
O. apertum (Verdoorn) Oberm.	BM	V 206, 314
O. hispidum Hornem.		
subsp. *hispidum*	BM	N 3969
O. pruinosum Leighton	BM	
O. secundum Jacq.	BM	V 221
O. suaveolens Jacq.	BM	V 259
O. cf. *unifolium* Retz.	BM	V 176
O. xanthochlorum Bak.	BM	N 121
Lachenalia Jacq. f. ex Murray		
L. anguinea Sweet	BM	V 304
L. mutabilis Sweet	BM	N 53 V 174
L. violacea Jacq.	BM	V 219
Massonia Thunb. ex Houtt.		
M. depressa Houtt.	BM	V 156
ASPARAGACEAE		
Asparagus L.		
A. capensis L. var. *capensis*	SM	N 75 V 256
A. exuvialis Burch.	SM	B
AMARYLLIDACEAE		
Haemanthus L.		
H. tristis	#BM$	B
known from only two localities in Tanqua		
Gethyllis L.		
G. cf. *verticillata* R. Br. ex Herb.	BM	V 172
G. cf. *villosa* (Thunb.) Thunb.	BM	B
TECOPHILAEACEAE		
Cyanella L.		
C. hyacinthoides L.	BM	V 220, 310

Table 5 (continued)

	Guilds	Identification
IRIDACEAE		
Moraea Mill.		
M. crispa Thunb.	*BM*	*V 217*
M. polystachya (Thunb.) er-Gawl.	*BM*	*B*
M. speciosa (L. Bol.) Goldbl.	*BM*	*V*
Ferraria Burm. ex Mill.		
F. uncinata Sweet	*BM*	*V 272*
Hesperantha Ker-Gawl.		
H. bachmannii Bak.	*BM*	*N 91*
Babiana Ker-Gawl.		
B. cf. *curviscapa* G.J. Lewis	*BM*	*V 182*
B. truncata G.J. Lewis	*BM*	*V 222*
Gladiolus L.		
G. permeabilis Delaroche	*BM*	*V 248*
G. scullyi Bak.	*BM*	*N 132*
Lapeirousia Purret		
L. plicata (Jacq.)	*BM*	*V 141*
L. pyramidalis (Lam.) Goldbl.	*BM*	*V 205 224*
URTICACEAE		
Forsskaolea L.		
F. candida L. f.	*SD*	*V 244*
SANTALACEAE		
Thesium L.		
T. lineatum L. f.	*SD*	
CHENOPODIACEAE		
Atriplex L.		
**A. lindleyi* Moq. subsp. *inflata* (F. Muell.) P.G. Wilson	*SD*	*N 3902*
Bassia All.		
Bassia salsoloides (Fenz.) A.J. Scott	*?SD*	*N 45, 67*
Salsola L.		
S. aphylla L. f	*SM*	*V 233, 289*
S. contrariifolia Botsch	*?SM*	*N*
S. cryptoptera Aell.	*?SD*	*N*
S. cf. *dealata* Botsch	*SD*	*V 264*
S. glabrescens Burtt Davy	*SD*	*B 79, 85*
**S. kali* L.	*E*	*V 243*
S. calluna Fenzl ex C.H. Wr. = *S. nigrescens* Verdoorn	*?SM*	*B*
S. rabieana Verdoorn	*?SM*	*N 21, 72*
S. tuberculata (Moq.) Fenzl	*SM*	*B, V 288*
S. zeyheri (Moq.) Schinz	*?SD*	*B*
AMARANTHACEAE		
Sericocoma Fenzl		
S. avolans Fenzl	*SM*	*V 216, 241*
S. pungens Fenzl	*SM*	*N 117*
AIZOACEAE		
Hypertelis E. Mey. ex Fenzl		
H. salsoloides (Burch.) Adamson	*E*	*B 3*
Plinthus Fenzl		
P. karooicus Verdoorn	*SD*	*V 215*
Galenia L.		
G. africana L. var. *africana*	*SD*	*N 15*
G. crystallina (Eckl. & Zeyh.) Fenzl var. *crystallina ?*	*E*	
G. fallax Pax	*?E*	*N 3921*
G. fruticosa (L. f.) Sond. var. *fruticosa*	*SD*	*V 261 137*
G. sarcophylla Fenzl	*E*	*V 293*
G. secunda (L. f.) Sond.	*?E*	*B*
Tetragonia L.		
T. echinata Ait.	*?SD*	*N 35*
T. fruticosa L.	*SD*	*V 183*
cf. *T. glauca* Fenzl	*?SD*	*N 58*
T. microptera Fenzl.	*SD*	*N*
T. sarcophylla Fenzl	*SD*	*V 225*
MESEMBRYANTHEMACEAE		
Arenifera spinescens (L. Bol.). H.E.K. Hartm	*VM*	*N*
Aridaria N.E. Br.		
A. noctiflora (L.) Schwant	*VM*	*B 84*
Aridaria sp.	*VM*	*V 239i*
Cephalophyllum N.E. Br.		
C. ebracteatum (Pax ex Schltr. & Dids)	*VG*	*V185*
Dinter & Schwantes		
Cheiridopsis N.E. Br.		
C. acuminata L. Bol.	*VG*	*V 159,211*
Drosanthemum Schwant.		
D. cymiferum L. Bol.	*VM$*	*B 74*
D. delicatulum (L. Bol.) Schwant.	*VM*	*B*
D. eburneum L. Bol.	*VM*	*V 157*
D. floribundum (Haw.) Schwant.	*VM*	*B 6, 46*
D. hispidum (L.) Schwant.	*VM*	*V 300*
D. lique (N.E. Br.) Schwant.	*VM*	*B 126*
D. subcompressum (Haw.) Schwant.	*VM*	*V 228, 235*
D. wittebergense L. Bol.	*VM*	*V 197,198,298*
Eurystigma L. Bol.		
E. clavatum (L. Bol.) L. Bol.	*#VM$*	*B N 41, 3939*
Hereroa Dinter ex Schwant.		
H. cf. *crassa*	*VM*	*B*
H. fimbriata L. Bol.	*VM*	*V 184, 208, 279*
H. odorata (L.Bol.) L. Bol	*VM*	*B*
Lampranthus N.E. Br.		
L. diffusus (L. Bol.) N.E. Br.	*VM*	*V 240*
Leipoldtia L. Bol.		
L. schultzei (Schltr. & Diels) Friedr.	*VM*	*V, B 73*
Malephora N.E. Br.		
M. luteola (Haw.) Schwant.	*VM*	*B 3914*
Mesembryanthemum L.		
M. chrysum L. Bol.	*VE*	*V 315*
M. crystallinum L.	*VE*	*V 255*
M. cf. *nodiflorum* L.	*VE*	*V 230*

Table 5 (continued)

	Guilds	Identification
M. pachypus L. Bol.	*VM*	*V 292*
M. cf. *stenandrum* (L. Bol.) L. Bol.	*VE*	*V 166, 209,196*
Prenia N.E. Br.		
P. pallens (Ait.) N.E. Br. subsp. *lancea* (Thunb.) Gerbaulet	*VM*	*N 3988*
Psilocaulon N.E. Br.		
P. absimile N.E. Br	*VM*	*V 179, 192*
P. cf. *pageae* L. Bol.	*VM*	*V 230b*
P. utile L. Bol	*VM*	*B*
Rhinephyllum N.E. Br.		
R. macradenium (L. Bol.) L. Bol.	*VM*	*V 212, 215b*
Ruschia Schwant.		
R. cradockensis (Kuntze) H.E.K. Hartman & Stüber subsp. *triticiformis* (L. Bolus) H.E.K. Hartm. & Stüber	*VM*	*B72*
R. erosa L. Bol.	*VM*	*V 276, 277*
R. cf. *herrei* Schwant.	*VM*	*V 290*
R. intricata (N.E. Br.) H.E.K. Hartm. & Stüber (Hartmann & Stüber 1993)	*VM*	*V 264*
R. cf. *karooica* (L. Bol.) L. Bol.	*VM*	*V 312*
R. cf. *robusta* L. Bol.	*VM*	*V*
R. spinosa (L.) Dehn	*VM*	*V214,278*
R. spinescens L. Bol.	*VM*	*N*
R. wittebergensis (L. Bol.) Schwant.	*VM*	*V*
Antimima N.E. Br.		
A. hantamensis (Engl.) H.E.K. Hartm. & Stüber	*VM*	*B 55*
Brownanthus Schwant.		
B. ciliatus (Ait.) Schwant.	*VM*	*B 57*
Phyllobolus N.E. Br.		
Phyllobolus sp.	*VM*	*V 202*
Tanquana H.E.K. Hartm. & Liede		
T. prismatica (Marloth) H.E.K. Hartm. & Liede	*#VM$*	*photo*
BRASSICACEAE		
Heliophila L.		
H. deserticola Schltr. var. *deserticola*	*E*	*N 51, V266*
H. digitata L. f.	*E*	*V 167*
CRASSULACEAE		
Cotyledon L.		
C. orbiculata L. var. *orbiculata*	*VM*	*B*
Tylecodon Toelken		
T. paniculatus (L. f.) Toelken	*VMS*	*N 3889a*
T. reticulatus (L. f.) Toelken	*VMS*	*photo*
T. wallichii (Harv.) Toelken	*VMS*	*V 159b*
Crassula L.		
C. deltoidea Thunb.	*VMS*	*B 63*
C. muscosa	*VM*	*V 281*

	Guilds	Identification
C. nudicaulis L. var. nudicaulis	*VM*	*N 3975*
C. subaphylla (Eckl. & Zeyh.) Harv.	*VM*	*V 171*
C. tomentosa Thunb. var. *glabrifolia* (Harv.) Rowley	*VM*	*N 3976*
C. umbellata Thunb.	*VG*	*V 294*
NEURADACEAE		
Grielum L.		
G. humifusum Thunb. var. *parviflorum* Harv.	*E*	*N 76 V 313*
FABACEAE		
Acacia Mill.		
A. karroo Hayne		
Crotalaria L.		
Crotalaria sp.	*L*	*V*
Prosopis L.		
**P. glandulosa* Torr.		
Lotononis (DC.) Eckl. & Zeyh.		
L. densa (Thunb.) Harv. subsp. *gracilis* (E.Mey.) B-E. van Wyk	*SM*	*V 190*
L. falcata (E. Mey.) Benth.	*E*	*N 70 V 270*
cf. *L. pungens* Eckl. & Zeyh.	*E*	*N 124*
Lebeckia Thunb.		
Lebeckia sp.	*?SM*	*N B*
Melolobium Eckl. & Zeyh.		
M. candicans (E. Mey.) Eckl. & Zeyh.	*SM*	*N 28, 3908*
M. exudans Harv.	*M*	*N 122*
M. microphyllum (L. f.) Eckl. & Zeyh.	*SM*	*V 237*
Sutherlandia R. Br. ex Ait. f.		
S. frutescens (L.) R. Br.	*SD*	*N 3948*
S. microphylla Burch. ex DC.	*SM*	*V 236*
Lessertia DC.		
L. annularis Burch.	*E*	*V 229*
L. pauciflora Harv. var. *pauciflora*	*?SD*	*N 123*
GERANIACEAE		
Sarcocaulon (DC.) Sweet		
S. crassicaule Rehm	*VMS*	*V 173*
S. salmoniflorum Moffett	*VMS*	*V 173b*
Pelargonium L'Hérit		
P. articulatum (Cav.) Willd.	*VMS*	*N 3977*
P. crithmifolium J.E. Sm.	*MS*	*V 254*
P. magenteum J.J.A. v.d.Walt	*VMS*	*N 100, V 253*
OXALIDACEAE		
Oxalis L.		
O. pes-caprae L.	*D*	*V 249*
O. pulchella Jacq.	*BD*	*V 151*
O. sonderiana (Kuntze) Salter	*BD*	*V 149*

Table 5 (continued)

	Guilds	Identification
ZYGOPHYLLACEAE		
Zygophyllum L.		
Z. lichtensteinianum Cham. & Schlechtd.	*SM*	*V 158*
Z. meyeri Sond.	*SM*	*N 93, V 301*
Z. microcarpum Licht. ex Cham. *& Schlechtd*	*SD*	*V 194, 218,268*
Z. retrofractum Thunb.	*SD*	*V 269*
Augea Thunb.		
A. capensis Thunb.	*VM*	*N 3890*
ANACARDIACEAE		
Rhus L.		
R. undulata Jacq.	*SM*	*N 94*
EUPHORBIACEAE		
Euphorbia L.		
E. decussata E. Mey. ex Boiss.	*VMS*	*V 280*
E. hamata (Haw.) Sweet	*VMS*	*photo*
E. mauritanica L.	*VMS*	*V 159a*
E. multiceps Berger	*VMS*	*B*
E. restituta N.E. Br. (id? Namaqualand coastal species)	*VMS*	*V 181*
STERCULIACEAE		
Hermannia L.		
H. cuneifolia Jacq. var. *cuneifolia*	*SD*	*N 106 V 195*
H. incana Cav.	*SD*	*B*
H. spinosa E. Mey. ex Harv.	*SD*	*V 246, 284*
THYMELAEACEAE		
Gnidia L.		
G. polycephala (C.A. Mey.) Gilg.	*SM*	*V 145, 186*
ASCLEPIADACEAE		
Microloma R. Br.		
M. sagittatum (L.) R. Br.	*L*	*V 163, 305*
Hoodia		
H. gordonii (Mass.) Sweet ex Decne.	*VMS*	*N 3916*
Stapelia L.		
Stapelia sp.	*VG*	*V (pers.obs.)*
HYDROPHYLLACEAE		
Codon L.		
C. royenii L.	*SD*	*N V 25,275*
BORAGINACEAE		
Trichodesma R. Br.		
T. africanum (L.) Lehm.	*E*	*N 113*
LAMIACEAE		
Salvia L.		
S. disermas L.	*?SD*	*N 3968*

	Guilds	Identification
SOLANACEAE		
Lycium L.		
L. bosciifolium Schinz	*SM*	*V*
L. cinereum Thunb. (sens. lat.)	*SM*	*V 140*
L. ferocissimum Miers	*SM*	*V 234*
SCROPHULARIACEAE		
Aptosimum Burch.		
A. indivisum Burch. ex Benth.	*SD*	*N 2*
A. procumbens (Lehm.) var. *procumbens*	*SD*	*B*
Peliostomum Benth.		
P. virgatum E. Mey. ex Benth.	*SD*	*N 110*
Nemesia Vent.		
N. fruticans (Thunb.) Benth.	*SD*	
N. karroensis Bond	*?SD*	*N 30*
N. ligulata E. Mey. ex Benth.	*E*	*V 165*
Manulea L		
Manulea cf. *latiloba* Hilliard.	*E*	*N 23*
Lyperia Benth		
Lyperia tristis (L. f.) Benth	*E*	*V 164*
Jamesbrittenia Kuntze		
Jamesbrittenia atropurpurea	*SD*	*N 114 V 191*
Zaluzianskya F.W. Schmidt		
Z. bella Hilliard	*#E*	*N 1*
Z. mirabilis Hilliard	*#E*	*N 82*
SELAGINACEAE		
Hebenstretia L.		
cf. *H. glaucescens* Schltr	*E*	*N 49*
H. parviflora E. Mey.	*E*	*V 168*
Selago L.		
S. albida Choisy	*SD*	*V 291*
LENTIBULARIACEAE		
Monechma Hochst.		
M. spartioides (T. Anders.) C.B. Cl.	*SD*	*N 81, 3910*
RUBIACEAE		
Anthospermum L.		
A. dregei Sond.	*SD*	*V 207*
Nenax Gaertn.		
N. cinerea (Thunb.) Puff	*SD*	*V 155*
CAMPANULACEAE		
Wahlenbergia Schrad. ex Roth		
W. androsacea A. DC.	*E*	*N 42, 86*
W. annularis A. DC.	*E*	*V 308*
LOBELIACEAE		
Cyphia Berg.		
C. bulbosa (L.) Berg.	*BD*	*V 213*
C. comptonii Bond	*#BD$*	*B 7*
ASTERACEAE		
Pteronia L.		
P. glabrata L. f.	*SM*	*N 90, V 146*

Table 5 (continued)

	Guilds	Identification
P. intermedia Phill. & Hutch	*SM*	*N 136 ,8*
P. leucoclada Turcz.	*SM*	*N 73*
P. lucilioides DC.	*SM*	
P. mucronata DC	*SM*	*V 287*
P. pallens L. f.	*SM*	*N 95*
P. punctata Phill.	*SM*	
P. quinqueflora DC.	*SM*	*V 153*
P. scariosa L. f.	*SM*	*N 80, 3909*
P. villosa L. f.	*SM*	*V 286*
P. viscosa Thunb.	*SM*	*N 104*
Amellus L.		
A. tridactylus DC. subsp. *arenarius* (S. Moore) Rommel	*E*	*V,N 3896,251*
A. tridactylus DC. subsp. *olivaceus* Rommel	*E*	*N, 10,48*
Felicia Cass.		
F. australis (Alston) Phill.	*E*	*V 299*
F. lasiocarpa DC.	*SD*	*V 311, 283*
Chrysocoma L.		
C. ciliata L.	*SD*	
cf. *Lasiopogon debilis* (Thunb.) Hilliard.	*B*	
Troglophyton Hilliard & Burtt		
T. parvulum (Harv.) Hilliard & Burtt	*?*	*N*
Helichrysum Mill.		
H. herniarioides DC.	*E*	*N 52 V 257*
Eriocephalus L.		
E. capitellatus DC.	*SD*	*V 265*
E. ericoides (L. f.) Druce	*SD*	*V 232*
E. spinescens Burch.	*SD*	*N 135*
Lasiospermum Lag.		
L. brachyglossum DC.	*?SD*	*N 37 ,2626*
Pentzia Thunb.		
P. incana (Thunb.) Kuntze	*SD*	
Oncosiphon Kallersjo		
O. grandiflorum (Thunb.) Kallersjö	*E*	*N 36 V 245*
O. piluliferum (L. f.) Kallersjö	*E*	*V 262, 297*
O. suffruticosum (L.) Kallersjö	*SD*	*N 3947, 3900*
Foveolina Kallersjö		
F. albida (DC.) Kallersjö	?	*N*
Cineraria L.		
C.cf. erosa (Thunb.) Harv.	*?E*	*N 83*
Senecio L.		
S. arenarius Thunb.	*?E*	*N 66*
S. cakilefolius DC.	*E*	*V 210*
S. cardaminifolius DC.	*E*	*V 203*
S. elegans L.	*E*	*pers.obs.*
S. sophioides DC.	*?E*	*N 17, 97*
Kleinia Mill.		
K. longiflora DC.	*VMS*	*N 92*
Euryops Cass.		
E. annuus Compton	*E*	*N 9*
Othonna L.		
O. arbuscula (Thunb.) Sch. Bip.	*VMS*	*N 105,77*
O. lobata Schltr.	*VMS*	*V 142*
O. protecta Dinter	*SM*	*N 15, 32*
O. pteronioides Harv.	*SM*	*B, 26*
O. spinescens DC.	*SM*	*V 154*
Osteospermum L.		
O. pinnatum (Thunb.) T. Norl. var. *pinnatum*	*E*	*N 24*
Tripteris Less.		
T. clandestina Less.	*E*	*N 39*
T. oppositifolium (Ait.) B. Nord.	*SM*	*V 226, 227*
T. sinuata DC. var. *sinuata*	*E*	*N 29*
Ursinia Gaertn.		
U. nana DC. subsp. *nana*	*E*	*N 38, V 252*
Arctotis L.		
A. hirsuta (Harv.) Beauv.	*E*	*N 13,20,78*
Gazania Gaertn.		
G. krebsiana Less. subsp. *arctotoides* (Less.) Roessl.	*SD*	*N 131*
G. krebsiana Less. subsp. *krebsiana*	*SD*	*N 33*
G. lichtensteinii Less.	*SD*	*B 3932*
G. tenuifolia Less.	*?E*	*N 69*
Hirpicium Cass.		
H. alienatum (Thunb.) Druce	*SD*	*V 285*
Berkheya Ehrh.		
B. fruticosa (L.) Ehrh.	*SD*	*N 107*
B. spinosa (L. f.) Druce	*SD*	*V 193, 250*

include 51 of the 54 succulent species listed in the phytosociological table (Table 1), including all the succulent plant species endemic to the Tanqua Karoo.

The number of species found in the Tankwa-Karoo National Park is 259 (Table 5), which accounts for almost 10 % of the total number of species provided in the list of Milton *et al.* (1997) and 5 % of the list of Hilton-Taylor (*pers. comm.*). The PRÉCIS databank provided a possible addition of 71 species and 36 genera for six quarter degree grid squares surrounding the park and stretching towards the Roggeveld Mountains. The park therefore seems to be a relevant conservation area, with the problem of localised endemics also ensuring that no one reserve or park would ever be considered representative of the entire Tanqua or succulent Karoo (Hilton-Taylor & Le Roux 1989).

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