Chapter 7

Plant diversity in the Hantam-Tanqua-Roggeveld, Succulent Karoo, South Africa: Diversity parameters

Abstract

Forty Whittaker plots were surveyed to gather plant diversity data in the Hantam-Tanqua-Roggeveld subregion of the Succulent Karoo. Species richness, evenness, Shannon's index and Simpson's index of diversity were calculated. Species richness ranged from nine to 100 species per 1000 m² (0.1 ha) with species richness for the Mountain Renosterveld being significantly higher than for the Winter Rainfall Karoo, which in turn was significantly higher than for the Tanqua Karoo. Evenness, Shannon and Simpson indices were found not to differ significantly between the Mountain Renosterveld and Winter Rainfall Karoo, however, these values were significantly higher than for the Tanqua Karoo. Species richness for all plot sizes <0.1 ha were significantly lower for the Tanqua Karoo than for the other two vegetation groups, which did not differ significantly from each other. Only at the 1000 m² scale did species richness differ significantly on the vegetation group level between the Mountain Renosterveld and the Winter Rainfall Karoo.

A Principal Co-ordinate Analysis (PCoA) of species richness data at seven plot sizes produced three distinct clusters in the ordination. One cluster represented the sparsely vegetated, extremely arid Tanqua Karoo which has a low species richness, low evenness values and low Shannon and Simpson indices. Another cluster represented the bulk of the Mountain Renosterveld vegetation with a high vegetation cover, high species richness, high evenness values and high Shannon and Simpson indices. The third cluster was formed by the remaining Mountain Renosterveld plots as well as the Winter Rainfall Karoo plots with intermediate values for the diversity parameters.

Keywords: Fynbos Biome, species evenness, Shannon index, Simpson index, species richness, Succulent Karoo Biome

7.1 Introduction

Despite changing fashions and preoccupations, diversity has remained a central theme to ecology (Magurran 1988). Diversity has two components: species richness, or the number of plant species in a given area, and species evenness, or how well abundance or biomass is distributed among species within a community (Wilsey & Potvin 2000). Numerous indices exist which use either species richness or evenness as well as a combination of these two components. In spite of various criticisms, these indices have sparked renewed interest in handling problems associated with the conservation of natural heritage or the changes in global ecology (Mouillot & Leprêtre 1999).

The Hantam-Tanqua-Roggeveld constitutes one of the four planning domains into which the Succulent Karoo was subdivided during the Succulent Karoo Ecosystem Plan (SKEP) initiative. In the course of the SKEP programme it soon became apparent that future planning of conservation and development in the subregion were hampered by a paucity of information available on the plant diversity (Cilliers et al. 2002, Critical Ecosystem Partnership Fund 2003). A study was therefore initiated to provide baseline information on patterns of plant diversity in this unique arid area. At the landscape level the diversity of plant associations have been described (Van der Merwe et al. 2008a, 2008b) and the species-area curves characterising the associations have been presented in Chapter 6.

The Succulent Karoo Biome is a predominantly winter rainfall arid region that occupies 111 000 km^2 on the fringes of South Africa's Cape Floristic Region (Mucina et al. 2006). The species richness of the Succulent Karoo flora is exceptional in terms of established hotspots, but especially in comparison with similar arid environments (Cowling & Hilton-Taylor 1994). Although the Roggeveld mountain range was included in the SKEP planning domain, there is some controversy as to whether it is actually part of the Fynbos Biome or the Succulent Karoo Biome (Marloth 1908, Diels 1909, Weimarck 1941, Hilton-Taylor 1994, Low & Rebelo 1996, Jürgens 1997, Van Wyk & Smith 2001, Mucina & Rutherford 2006) or even Nama Karoo Biome (Rutherford & Westfall 1994). The Fynbos Biome as delineated by Rutherford and Westfall (1994) constitutes the major portion of the Cape Floristic Region (CFR). The CFR is recognised as one of the world's plant kingdoms (Good 1947) and is additionally recognised as a global hotspot of diversity (Cowling & Hilton-Taylor 1994). There is a close affiliation between the Succulent Karoo and Fynbos Biomes and Jürgens (1997) proposed the recognition of the Floristic Kingdom of the Greater Cape Flora including at least two partial areas, the Cape Floristic Region and the Succulent Karoo Region. Similarly, Born et al. (2007) investigated the concept of the Greater Cape Floristic Region, which includes the whole winter rainfall area of southern Africa (arid and mesic climates).

The present paper aims to analyse the patterns in the plant diversity of the Hantam, Tanqua and Roggeveld areas in terms of species richness at different scales, species evenness and the Shannon and Simpson indices of diversity.

7.2 Study area

The Succulent Karoo occurs in the western regions of Namibia and South Africa (Milton et al. 1997). It is an area of high plant species diversity at both the local and regional scales (Cowling et al. 1989) and high levels of plant endemism. Within the Hantam-Tanqua-Roggeveld study area Hilton-Taylor (1994) identified three centres of endemism and Van Wyk and Smith (2001) recognised the Hantam-Roggeveld as one of the 13 principal regions and centres of plant endemism in southern Africa.

The Hantam, Tanqua and Roggeveld as defined in this study, lie in the predominantly winter rainfall region of the Northern and Western Cape Provinces of South Africa and cover an area of approximately three million hectares (Figure 7.1). Although the rain falls mainly in winter it does include a few summer thunderstorms with the mean annual precipitation in the subregion ranging from <100 mm to 467 mm per year, the maximum measured for Sutherland (Schulze 1997, Weather Bureau 1998).

Figure 7.1 Location of the Hantam-Tanqua-Roggeveld subregion in South Africa.

Topographically, the three regions differ vastly with the Hantam characterised by a gently undulating to a steeply rolling topography, with the exception of the flat-topped Hantam Mountain rising steeply above the flat surroundings of the town of Calvinia. The Tanqua Karoo covers vast plains from where the landscape rises steeply to the escarpment formed by the Roggeveld, Komsberg and Nuweveld Mountains. The Roggeveld plateau stretches eastwards from the escarpment into the interior of South Africa. Altitude varies from approximately 290 m above sea level in the Tanqua Karoo to about 1800 m above sea level on the high-lying areas along the Roggeveld Mountain Range.

Shallow lithosols and duplex soils characterise the Hantam Karoo, while scattered dolerite intrusions produce red structural and red vertic clays. The Tanqua Karoo soils are comprised of shallow lithosols that often include deep unconsolidated deposits in the alluvial parts or desert pavement. Soils of the Hantam Mountains and the mountains of the great escarpment are shallow stony lithosols. The occasional lowlands contain duplex soils (Francis et al. 2007).

The study area includes three of Acocks's (1953, 1988) veld types namely: Mountain Renosterveld, Succulent Karoo and Western Mountain Karoo. The Mountain Renosterveld, as defined by Acocks is equivalent to the Escarpment Mountain Renosterveld of Low and Rebelo (1996). While Acocks's Succulent Karoo and Western Mountain Karoo form part of the Lowland Succulent Karoo and Upland Succulent Karoo of Low and Rebelo (1996) respectively. The latest vegetation map of South Africa (Mucina et al. 2005, Mucina & Rutherford 2006), identified 12 vegetation types within the area. A recent phytosociological classification of the area recognised eight major plant associations and 25 subassociations in the study area (Van der Merwe et al. 2008a, 2008b).

7.3 Materials and methods

Forty sample plots were surveyed across the Hantam, Tanqua and Roggeveld regions in each of the eight vegetation associations described in the area (Van der Merwe et al. 2008a, 2008b). Altitude, aspect, slope, position on the slope, geology, topography, percentage stone and stone size, soil type and colour, drainage, erosion, trampling and soil compaction are some of the environmental data noted at each plot.

Field surveys were conducted using Whittaker's plant diversity plot technique (Shmida 1984) with the only modification being the field form and notations used on the field form (see Chapter 6 for more detail). The presence of each species encountered in a quadrat was noted within a column and a cover value was assigned to each species for the 1000 m² quadrat. Seven different plot sizes were used for comparisons of species richness. The total species number for each of the seven plot sizes (1 m², 5 m², 10 m², 20 m², 50 m², 100 m² and 1000 m²) were determined by using the mean of the ten 1 m² plots for the 1 m² plot, a mean of the two 5 m² plots for the 5 m² plot, mean of the total of ten 1 m² plots and the total of two 5 m² plots for the 10 m² plot, total of the ten 1 m² and the two 5 m² plots for a 20 m² plot, a mean of the two 50 m² plots for a 50 m² plot, the total of the two 50 m² plots for a 100 m² plot and the total for the 1000 m² plot.

Species richness (S), Shannon's index of diversity (H'), Simpson's index (D) and a measure of evenness (E) were calculated for each sampled plot at the 1000 m² (0.1 ha) size, using the PC-ORD computer program (PC-ORD Version 4 for Windows, MjM Software design) which calculates these four diversity measures as follows:

S = richness = number of non-zero elements in a sampling unit.

H' = Shannon diversity

$$H' = -\sum_{i}^{S} p_i \log p_i$$

Where p_i = importance probability in column *i*.

E = Evenness (equitability) = H' / ln (richness)

D = Simpson's index of diversity for an infinite population. This is the complement of Simpson's original index and represents the likelihood that two randomly chosen individuals will be different species.

$$D = 1 - \sum_{i}^{S} p_i{}_i^2$$

Comparisons are made throughout the paper with respect to the eight main vegetation associations as described in Van der Merwe et al. (2008a, 2008b). Additionally, comparisons are made at a higher hierarchical level for which purpose some of the associations were grouped into vegetation groups. The three Mountain Renosterveld associations are grouped together and called Mountain Renosterveld, the Escarpment Karoo, Hantam Karoo and Roggeveld Karoo are collectively referred to as the Winter Rainfall Karoo and the Tanqua and Loeriesfontein Karoo together with the Central Tanqua Grassy Plains are termed Tanqua Karoo.

The STATISTICA computer package was used to conduct the statistical analyses (StaSoft, Inc. Version 7 and 8, 2300 East 14th Street, Tulsa, OK 74104). One-way Analysis of Variance (ANOVA) (Bonferroni's *post-hoc* test), were performed to determine significant differences in diversity parameters between the vegetation associations and between species richness at different plot sizes (1 m², 5 m², 10 m², 20 m², 50 m², 100 m², 1000 m²). All ANOVAs were preceded by a test for normality. The total number of species for all seven plot sizes for the forty survey plots were ordinated using Principal Co-ordinate Analysis (PCoA) in the SYN-TAX computer program (Podani 2001).

7.4 Results and discussion

Species richness, or the number of species, remains the most widely used diversity measure (Stirling & Wilsey 2001) because it is relatively easy to measure, is comparable across communities, and is well understood by researchers, managers, and the public (Hellman & Fowler 1999). Richness at the 1000 m² level is regarded as a measure of alpha or within-habitat diversity (Whittaker 1977, Cowling et al. 1989, 1992) although significant turnover or internal beta diversity may be associated with habitat heterogeneity at this scale (Cowling et al. 1989).

In this study, the species richness values ranged from nine to 100 species per sampled 1000 m² (Table 7.1). The species richness of Mountain Renosterveld (mean: 79, range: 62-99 species, Table 1) was found to be significantly higher than that of the Winter Rainfall Karoo (mean: 64.6, range: 31-100 species), which in turn was significantly higher than that of the Tanqua Karoo (mean: 18.6, range: 9-30 species, Table 7.1) (Table 7.2). An analysis of the data at 1000 m² for each vegetation association did not produce significant differences ($p > 0.05$).

Table 7.1 Vegetation group, plant association number, survey plot number, species richness, species evenness, Shannon's and Simpson's index of diversity for 40 plots surveyed in the Hantam-Tanqua-Roggeveld subregion in 2005

Vegetation group	Plant asso-ciation no.	Survey plot no.	Species richness	Evenness (E)	Shannon index (H')	Simpson index (D)
Mountain Renosterveld	1	W23	99	0.794	3.647	0.9431
Mountain Renosterveld	1	W24	72	0.759	3.248	0.9265
Mountain Renosterveld	1	W25	65	0.533	2.225	0.6770
Mountain Renosterveld	1	W26	82	0.635	2.797	0.7877
Mountain Renosterveld	1	W27	70	0.563	2.392	0.7267
Mountain Renosterveld	2	W3	75	0.587	2.533	0.7833
Mountain Renosterveld	2	W4	72	0.745	3.186	0.9158
Mountain Renosterveld	2	W11	62	0.572	2.360	0.7327
Mountain Renosterveld	2	W12	65	0.501	2.091	0.6042
Mountain Renosterveld	2	W20	79	0.706	3.087	0.8965
Mountain Renosterveld	2	W21	84	0.630	2.791	0.7798
Mountain Renosterveld	2	W28	96	0.820	3.743	0.9439
Mountain Renosterveld	2	W29	85	0.641	2.849	0.8403
Mountain Renosterveld	2	W30	93	0.544	2.464	0.6668
Mountain Renosterveld	2	W40	66	0.595	2.493	0.7644

Table 7.1 (continued)

Mountain Renosterveld	3	W7	79	0.656	2.868	0.8432
Mountain Renosterveld	3	W8	99	0.779	3.582	0.9160
Winter Rainfall Karoo	4	W5	90	0.669	3.009	0.8170
Winter Rainfall Karoo	4	W6	100	0.585	2.693	0.6967
Winter Rainfall Karoo	4	W38	70	0.506	2.150	0.7244
Winter Rainfall Karoo	4	W39	68	0.554	2.338	0.7185
Winter Rainfall Karoo	5	W9	63	0.505	2.092	0.6629
Winter Rainfall Karoo	5	W10	74	0.612	2.633	0.8033
Winter Rainfall Karoo	5	W31	57	0.513	2.074	0.7108
Winter Rainfall Karoo	5	W32	47	0.539	2.076	0.7493
Winter Rainfall Karoo	5	W33	61	0.503	2.066	0.5813
Winter Rainfall Karoo	5	W34	62	0.674	2.783	0.8367
Winter Rainfall Karoo	5	W35	35	0.639	2.273	0.8525
Winter Rainfall Karoo	5	W36	71	0.622	2.650	0.8303
Winter Rainfall Karoo	5	W37	79	0.723	3.158	0.9001
Winter Rainfall Karoo	6	W1	60	0.560	2.294	0.7401
Winter Rainfall Karoo	6	W2	66	0.563	2.358	0.6542
Winter Rainfall Karoo	6	W22	31	0.606	2.081	0.7279
Tanqua Karoo	7	W13	30	0.415	1.143	0.4485
Tanqua Karoo	7	W14	26	0.668	2.178	0.8042
Tanqua Karoo	7	W17	13	0.742	1.902	0.7348
Tanqua Karoo	7	W19	26	0.493	1.607	0.6616
Tanqua Karoo	8	W15	14	0.170	0.450	0.1448
Tanqua Karoo	8	W16	12	0.473	1.176	0.5105
Tanqua Karoo	8	W18	9	0.065	0.144	0.0429

On a biome scale, Cowling et al. (1989) reported the highest mean species richness values per 1000 m^2 for Renosterveld (86), Grassland (82) and Succulent Karoo (74), whereas the biomes with the most species-poor communities were forest (51) and Nama Karoo (47). Within the Fynbos Biome richness in 1000 m^2 plots ranged from 21 in the southern Fynbos to 142 in the renosterveld (Cowling et al. 1989). Since the Tanqua Karoo is located within the Succulent Karoo Biome, the mean species richness value of 18.6 found in the current study is very low compared to the mean value of 74 species per 1000 m^2 (Cowling et al. 1989) and mean value of between 42.5 and 49.8 (Anderson & Hoffman 2007), and the maximum value of 113 species per 1000 m^2 found by Cowling et al. (1989). The mean value determined in this study for the Winter Rainfall Karoo which is also part of the Succulent Karoo, lies between mean values cited by Cowling et al. (1989) and Anderson & Hoffman (2007). However, the 2005 year in which the data in the current study were collected was a very poor rainfall year that would have had a severely negative impact on the species richness (see Aronson & Shmida 1992) since annual and geophytic species constitute a large component of the Succulent Karoo diversity.

According to Low and Rebelo (1996) and Mucina et al. (2005), the Mountain Renosterveld is located in the Fynbos Biome even though it has been included in SKEP's Succulent Karoo delineation. Born et al. (2007) demarcated the area as part of a proposed Greater Cape Floristic Region and mentioned its transitional nature. One 1000 m² plot in the Cape Floristic Region normally holds approximately 65 to 68 species (Cowling et al. 1992, Cowling & Holmes 1992, Procheş et al. 2003). A mean of 66 (range: 31-126) species per 1000 m² was found at 40 fynbos sites distributed throughout the fynbos region (Richardson et al. 1995). In the renosterveld vegetation mean values of 66 (Tilman et al. 1983), 84 (Cowling & Holmes 1992) and 60 (Kongor 2009) have been recorded. The mean species richness of 79 (range: 62-99) determined in this study compares well with the mean values reported for renosterveld. Mean species richness for sclerophyllus shrublands and woodlands from the South West Botanical Province in Western Australia is about 69 species which is comparable with fynbos values, whereas chaparral of the California Floristic Province is poorer in species with a mean of 30 species per 1000 m² (Cowling et al. 1992).

Table 7.2 Mean values and significance for species richness, species evenness, Shannon index and Simpson index within the Mountain Renosterveld, Winter Rainfall Karoo and Tanqua Karoo vegetation groups. Within a column values with the same superscript do not differ significantly at α = 0.05

Vegetation group	Species richness	Evenness (E)	Shannon index (H')	Simpson index (D)
Mountain Renosterveld	79.0[a]	0.65[a]	2.84[a]	0.81[a]
Tanqua Karoo	18.6[b]	0.43[b]	1.27[b]	0.48[b]
Winter Rainfall Karoo	64.6[c]	0.59[a]	2.42[a]	0.75[a]

Using seven different plots sizes (1 m², 5 m², 10 m², 20 m², 50 m², 100 m², 1000 m²) comparisons in species richness were made across the range of vegetation groups (Mountain Renosterveld, Winter Rainfall Karoo and Tanqua Karoo). A one-way ANOVA, indicated that there was a significant difference between Winter Rainfall Karoo and Mountain Renosterveld only at the 1000 m² plot size (Table 7.3). Significant differences were found between the Tanqua Karoo and Winter Rainfall Karoo as well as Mountain Renosterveld and Tanqua Karoo for all smaller plot sizes (Table 7.3). The fact that a significant difference between the Winter Rainfall Karoo and Mountain Renosterveld was only encountered at the 1000 m² (0.1 ha) plot size, indicates the importance of surveying relatively large plots to pick up differences in species richness. Therefore, most phytosociological data collected in South Africa at plot sizes of 200 m² or smaller, would be insufficient to pick up differences in species richness between vegetation groups. Although a study of 0.1 ha data from local inventories each sampled intensively on single occasions at a suite of scattered locations, provides data for comparisons of variation in species richness across geographical space (Clinebell et al. 1995) it remains a local (alpha) scale study, likely to retain signal factors that vary measurably on local scales, such as soil nutrient status (Whittaker et al. 2001).

Table 7.3 Mean species richness values for a range of plot sizes within three vegetation groups in the Hantam-Tanqua-Roggeveld subregion. Within a column values with the same superscript do not differ significantly at $\alpha = 0.05$

Vegetation group	**1 m² plot**	**5 m² plot**	**10 m² plot**	**20 m² plot**	**50 m² plot**	**100 m² plot**	**1000 m² plot**
Mountain Renosterveld	12.9[a]	21.6[a]	31.1[a]	38.3[a]	39.9[a]	49.7[a]	79.1[a]
Tanqua Karoo	2.2[b]	3.5[b]	5.4[b]	6.6[b]	7.3[b]	8.9[b]	18.6[b]
Winter Rainfall Karoo	9.5[a]	16.2[a]	25.0[a]	30.9[a]	32.5[a]	41.1[a]	64.6[c]

Evenness (E) is a measure of the ratio of observed diversity to maximum diversity (Magurran 1988). A 13-fold range of evenness values was obtained for the 1000 m² (0.1 ha) plots across the entire study area. The values ranged from 0.065 in the Tanqua Karoo (plot W18) to 0.820 in the Mountain Renosterveld (plot W28) (Table 1). Evenness is constrained between 0 and 1.0 with 1.0 representing a situation in which all species are equally abundant (Magurran 1988). In all except two cases, evenness was found to be larger than 0.4 (Table 7.1). Species evenness in the Mountain Renosterveld and Winter Rainfall Karoo was significantly higher than in the Tanqua Karoo (Table 7.2). The evenness values for the Tanqua Karoo plots were generally less than 0.5 except for survey plot W14 (0.668) and plot W17 (0.742) (Table 7.1), whereas evenness values for the Winter Rainfall Karoo and Mountain Renosterveld ranged from 0.501 (plot W12) to 0.820 (plot W28) (Table 7.1).

Both the Shannon index of diversity (H’) and the Simpson index (D) take evenness and species richness into account. The rankings of these two measures of diversity were fairly similar and the relationship between these parameters in the study area could best be described by a logarithmic equation ($y = 0.3048 \ln(x) + 0.4915$; $r^2 = 0.8816$). The Shannon index assumes that individuals are randomly sampled from an indefinitely large (that is an effectively infinite) population and that all species in the community are accounted for in the sample (Magurran 1988). However, it is likely that several species in the community will have been missed in the sampling effort and thus, the number of species found in the sample must be regarded as the lower bound to the number of species in the population (Heltshe & Forrester 1983). In general, the Shannon diversity index ranges between 1.5 and 3.5 and only rarely surpasses 4.5 (Magurran 1988). The original Simpson index (D) was referred to as a dominance measure since it was weighted towards the abundances of the commonest species rather than providing a measure of species diversity (Magurran 1988). In this study the complement of the original dominance measure (1 – D) was used to provide an estimate of diversity.

The indices derived in this study are believed to be underestimates of the potential values because of poor rainfall conditions in 2005 when the data were collected. The values for the Shannon index ranged 26-fold across the study area from 0.144 (plot W18, Tanqua Karoo) to 3.743 (plot W28, Mountain Renosterveld) (Table 7.1), however, all values, except for two survey plots (W15 and W18, both Tanqua Karoo), were > 1.0. The mean Shannon index value for the Tanqua Karoo was significantly lower than that for the Winter Rainfall Karoo and Mountain Renosterveld (Table 7.2). No significant difference was found for the Shannon index between the latter two vegetation groups.

The range of Simpson index values found for this study varied from 0.0429 (plot W18, Tanqua Karoo) to 0.9439 (plot W28, Mountain Renosterveld) (Table 7.1). The mean Simpson index values of the Mountain Renosterveld and Winter Rainfall Karoo were significantly higher than those of the Tanqua Karoo, however, there was no significant difference in the Simpson index values between the Mountain Renosterveld and Winter Rainfall Karoo (Table 7.2).

To analyse the patterns with respect to the data of the seven plot sizes for the 40 survey plots simultaneously, a Principal Co-ordinate Analysis (PCoA) was done. The resulting PCoA shows three distinct clusters (Figure 7.2). The first axis on the ordination diagram can be interpreted as an aridity gradient, which largely coincides with an altitudinal gradient. The cluster formed on the left hand side of the ordination represents a selection of Mountain Renosterveld plots and includes plots W5 and W6 which were surveyed on the Gannaga Mountain Pass (*Pteronia glauca – Euphorbia decussata* Escarpment Karoo) in the transition between the Mountain Renosterveld and Tanqua Karoo vegetation groups. This cluster of plots represents the high-lying vegetation, generally between 1020 m and 1421 m above sea level, with a high plant cover of 75 - 98% and sandstone of the Waterford Formation (Johnson et al. 2006) present in the environment. The analysis of the species-area curves for these plots revealed a combination of steep slopes and high y-intercept values for most plots (Chapter 6). The cluster formed on the right hand side of the ordination scatterplot represents the Tanqua Karoo survey plots (Figure 7.2). The low species richness values with respect to all seven plot sizes clearly distinguish this cluster from the other clusters. These survey plots are characterised by a low plant cover, generally between 10 and 60%, found on shales at an altitude of 374 to 647 m above sea level. Slopes of species-area curves for these plots were shallow and the values for the y-intercept low (Chapter 6). With the exception of the two plots on the Roggeveld escarpment all other plots surveyed in the Winter Rainfall Karoo belonged to the central cluster. However, several Mountain Renosterveld plots also fell within this cluster.

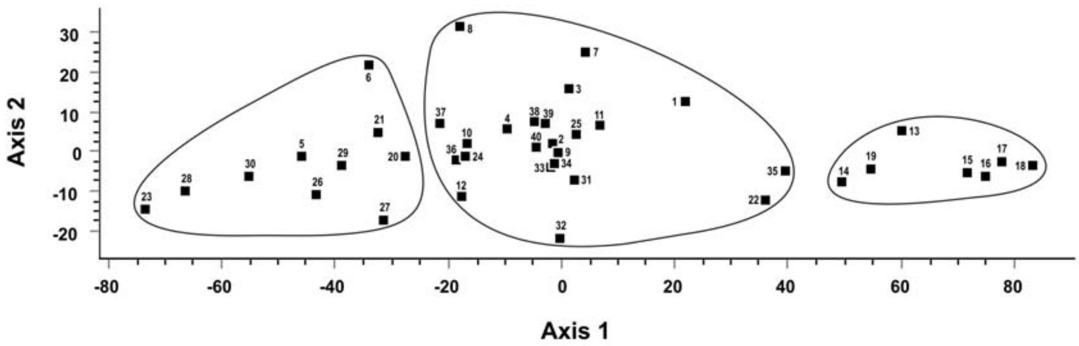

Figure 7.2 A Principal Co-ordinate Analysis (PCoA) scatterplot of species richness values for seven plot sizes on 40 plots surveyed in 2005 in the Hantam, Tanqua and Roggeveld areas. Numbers denote the survey plot numbers.

The ordination confirms that the Tanqua Karoo vegetation is very different from the vegetation in the rest of the study area and provides for interesting observations with respect to the Mountain Renosterveld of the subregion. The left hand cluster is comprised of the 'true' Mountain Renosterveld plots separating them from the centre cluster. This 'true' Mountain Renosterveld occurs on sandstones of the Waterford Formation (Johnson et al. 2006) and is assumed to be more closely related to the renosterveld of the Fynbos Biome. The centre cluster comprised of the Winter Rainfall Karoo plots, however also includes Mountain Renosterveld plots, indicating a strong link with the Succulent Karoo Biome.

7.5 Conclusions

Forty Whittaker sample plots were surveyed throughout the Mountain Renosterveld, Winter Rainfall Karoo and Tanqua Karoo vegetation groups of the Hantam, Tanqua and Roggeveld regions.

Species richness in the 1000 m² plots ranged from nine to 100 species per sampled 1000 m² among the 40 plots. Mean species richness was significantly lowest in the Tanqua Karoo and significantly highest in the Mountain Renosterveld vegetation. Mean species richness values of the Tanqua Karoo compared poorly with Succulent Karoo values cited in the literature. Species richness values for the Mountain Renosterveld compared well with values obtained for the renosterveld of the Fynbos Biome. However, the 2005 year in which the survey was conducted was a very poor rainfall year which would have had a negative impact on annual and geophyte species that make up a large component of Succulent Karoo and Fynbos Biome diversity.

Evenness values for the Tanqua Karoo were generally less than 0.5 and significantly less than the 0.501 to 0.820 for the Winter Rainfall Karoo and Mountain Renosterveld vegetation.

Similarly, the Shannon indices for the Tanqua Karoo (0.144 to 1.902) were significantly lower than those for the Winter Rainfall Karoo and Mountain Renosterveld (2.066 to 3.743). The Simpson indices varied from 0.0429 to 0.9439 across the study area and also indicated that the values for the Tanqua Karoo were significantly lower than those for the other two vegetation groups. No significant differences could be found between the Winter Rainfall Karoo and Mountain Renosterveld regarding either evenness, Shannon's or Simpson's index. In contrast, the species richness in 1000 m^2 plots of the Mountain Renosterveld was significantly higher than that of the Winter Rainfall Karoo, which in turn was significantly higher than that of the Tanqua Karoo. At all other plot sizes (1 m^2, 5 m^2, 10 m^2, 20 m^2, 50 m^2, and 100 m^2) significant differences were found in species richness between each plot size for the Winter Rainfall Karoo and Tanqua Karoo and the Mountain Renosterveld and Tanqua Karoo vegetation groups, but not between the Winter Rainfall Karoo and Mountain Renosterveld.

Species richness is still commonly used as a measure of diversity, however, species richness provides relatively little information and is a relatively coarse measure of diversity. If used on its own, and only measured at one plot size then care should be taken to determine the size of the plot needed to detect differences. Information gained from species counts is far more valuable if determined at different plot sizes because this allows the construction of species-area curves or the application of ordination techniques.

A Principal Co-ordinate Analysis (PCoA) of the sample plots, using species richness data for the seven plot sizes produced three distinct clusters. The one cluster was formed by the sparsely vegetated, arid, low-altitude Tanqua Karoo plots, while another cluster was formed by the Mountain Renosterveld plots found predominantly at high altitudes on sandstone of the Waterford Formation with a high vegetation cover. The centre cluster was formed by a combination of Winter Rainfall Karoo and Mountain Renosterveld vegetation groups. This ordination indicates that the way in which the species accumulate with an increase in size sampled of some of the Mountain Renosterveld plots is similar to the species accumulation pattern of the Succulent Karoo plots. However, there is a group of Mountain Renosterveld plots in the Hantam-Tanqua-Roggeveld subregion where the species accumulation pattern differs and these plots could possibly show affinities to the Fynbos Biome.

Information on species richness values and diversity indices gained in the study can be used to guide conservation efforts in the Hantam-Tanqua-Roggeveld subregion. For example, associations 7 and 8 are two of the most species poor associations, with the lowest levels of diversity, yet, they dominate the area conserved within the Tankwa Karoo National Park. The Tankwa Karoo National Park also includes, to a very limited extent, a small area of associations 2 and 4 which both have a high level of diversity. These areas could be notably expanded and the goal of the Tankwa Karoo National Park could be to include areas within associations 1 and 6. This would then actively conserve six of the eight associations in the Hantam-Tanqua-Roggeveld subregion, including some of the most diverse associations in the region.

7.6 Acknowledgements

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Chapter 8

Plant diversity in the Hantam-Tanqua-Roggeveld, Succulent Karoo, South Africa: Life form spectra

Abstract

The Hantam-Tanqua-Roggeveld subregion is situated in a predominately winter rainfall area of the Succulent Karoo and Fynbos Biomes of South Africa. These biomes are both recognised as global hotspots of diversity with high species diversities at local and regional scales.

Life forms are closely related to climate and habitat and are often used as a trait to group species growing under certain environmental conditions together. In general, the eight plant associations found in the study area were dominated by chamaephyte, cryptophyte (geophyte) and therophyte species.

At a species level, phanerophyte contributions were lower in the Winter Rainfall Karoo and Tanqua Karoo than in the Mountain Renosterveld. Cryptophyte contributions were higher in the Mountain Renosterveld than in the Tanqua Karoo. Similar hemicryptophyte contributions were found in the Mountain Renosterveld and Winter Rainfall Karoo vegetation with slightly higher values obtained for the Tanqua Karoo. Therophyte contributions were similar in the Mountain Renosterveld and the Winter Rainfall Karoo and significantly less in the Tanqua Karoo.

On a vegetation cover level, the phanerophyte contributions were significantly highest in the Mountain Renosterveld and lowest in the Tanqua Karoo. Chamaephyte cover varied greatly with the cover in the Mountain Renosterveld and Winter Rainfall Karoo significantly higher than in the Tanqua Karoo. Hemicryptophyte, liana and parasite cover contributions were the least. Cryptophyte cover was high for Mountain Renosterveld and Winter Rainfall Karoo and lower for the Tanqua Karoo as was therophyte cover yet no statistical significance was found.

Since the Succulent Karoo Biome is known for its succulents, the degree of succulence was compared among the vegetation associations and broad vegetation groups. Succulent species were found mostly in the chamaephyte, hemicryptophyte and therophyte life form categories. The contribution of succulents on a species level was significantly lowest in the Mountain Renosterveld and highest in the Winter Rainfall Karoo and Tanqua Karoo vegetation, with a higher than expected vegetation cover for the succulent life form in a strongly Mountain Renosterveld (Fynbos Biome) association, indicating its transitional nature between the two biomes.

A comparison of life form spectra with another site in the Succulent Karoo, Goegap Nature Reserve, produced more similar patterns than a comparison with another winter rainfall desert, the Mojave Desert. The Mountain Renosterveld life form spectra compared poorly to another Fynbos Biome site at Swartboskloof.

Keywords: Fynbos Biome, Mountain Renosterveld, succulence, Succulent Karoo Biome, Tanqua Karoo, Whittaker plots, Winter Rainfall Karoo

8.1 Introduction

The Hantam-Tanqua-Roggeveld subregion was one of the subregions delineated for management purposes during the Succulent Karoo Ecosystem Plan (SKEP) initiative in 2002. This initiative was launched to identify and generate consensus for a 20-year conservation and sustainable land use strategy for the Succulent Karoo hotspot of biodiversity (Conservation International – website).

Three biomes namely: the Fynbos, Succulent Karoo and Nama Karoo Biomes (Rutherford and Westfall 1994), meet in the vicinity of the Hantam-Tanqua-Roggeveld subregion. The transitional nature of the area has lead to some controversy as to whether the vegetation, especially that of the Roggeveld, should be classified as belonging to the Fynbos (Low & Rebelo 1996, Mucina et al. 2005, Rebelo et al. 2006, Rutherford et al. 2006) or Succulent Karoo Biome (Hilton-Taylor 1994, Jürgens 1997, Van Wyk & Smith 2001) or even the Nama Karoo Biome (Acocks 1988, Rutherford & Westfall 1994). A recent paper by Born et al. (2007) on the validity of the recognition of a Greater Cape Floristic Region also highlights the area's transitional nature.

Globally, there are few other areas that can claim to be as biologically distinct as the Succulent Karoo Biome (Milton et al. 1997, Cowling & Pierce 1999, Mucina et al. 2006), with this biome being recognised by the IUCN as one of the global hotspots of diversity (Myers et al. 2000, Critical Ecosystem Partnership Fund 2003). The Succulent Karoo Biome is an arid area and plant species diversity at both local and regional scales is reported to be the highest recorded for any arid region in the world (Cowling et al. 1989).

For the most part the Cape Floristic Region (CFR) comprises the Fynbos Biome. The Cape flora's unique species composition has led it to be recognised as one of the world's floristic kingdoms (Good 1947), on par with much larger regions (Rebelo et al. 2006). This region is also recognised as a global hotspot of biodiversity with one of the highest species densities and levels of endemism, at both local and regional scales, for temperate or tropical continental regions (Cowling et al. 1989, 1992, Cowling & Hilton-Taylor 1994).

The most common, parsimonious and accepted plant life form classification is Raunkiaer's (1934) (Van Rooyen et al. 1990, Pavón et al. 2000) who suggested that the location of a plant's renewal buds, as differentiated in various life forms, best expresses its adaptation to the unfavourable season for plant life (Danin & Orshan 1990). Because plant architecture and physiognomy can often be linked to the different climatic or environmental conditions under which a species grows and certain life forms are restricted to growing in particular habitats (Barbour et al. 1999), a life form spectrum of a region can give preliminary information concerning the habitat and the adaptive suite of plant traits occurring there.

Although life form spectra based on the total flora of a sufficiently large area are useful in the indication of the general or prevailing phytoclimate within such an area, the effects of local environments (microclimates and edaphic conditions) are best revealed when the spectra are modified by the use of quantitative data on the roles of various species in the respective local communities (Cain 1950, Danin & Orshan 1990). Life form studies have shown that the distribution and abundance of different plant life forms have well defined limits along altitudinal gradients and suggest that environmental heterogeneity in semi-arid environments contributes to the diversity of life forms, thus affecting community physiognomy and structure (Pavón et al. 2000). Additionally, assessing effects of climate change by life form or plant functional types (PFTs) is increasingly being applied to identify future trends in ecosystem structure (Broennimann et al. 2006).

The aim of this study was to compare life form spectra at a species as well as a vegetation cover level at the scale of three broad vegetation groups and eight plant associations found in the Hantam-Tanqua-Roggeveld study area. A degree of succulence was calculated and also used in an attempt to provide clarity on the Succulent Karoo vs. Fynbos Biome affinities of the vegetation in the Hantam-Tanqua-Roggeveld subregion.

8.2 Study area

The Hantam-Tanqua-Roggeveld subregion is situated in the predominantly winter rainfall area of the Northern and Western Cape Provinces of the Republic of South Africa (Figure 8.1). Although the rains fall mainly in winter, a few summer thunderstorms do occur. Rainfall ranges from 25 mm in parts of the Tanqua Karoo to 467 mm per year, the maximum recorded for Sutherland in the Roggeveld area (Weather Bureau 1998).

Rocks of the Ecca Group cover most of the area and include sediments of the Koedoesberg Formation (sandstone and shale) and the Tierberg Formation (shale), (Council for Geoscience 2008). The Dwyka Group consisting of tillite, sandstone, mudstone and shale crops out in the west of the study area with the mudstones of the Beaufort Group found on the eastern side of the study area (Council for Geoscience 2008). Igneous rock intrusions of dolerite occur throughout the region.

The Hantam is characterised by shallow lithosols and duplex soils, while red structural and vertic clays are produced by the scattered dolerite intrusions. Soils of the Tanqua Karoo are shallow lithosols that often include deep unconsolidated deposits in the alluvial parts or desert pavement. The soils of the great escarpment and Hantam Mountains are shallow stony lithosols with the occasional lowlands comprised of duplex soils (Francis et al. 2007).

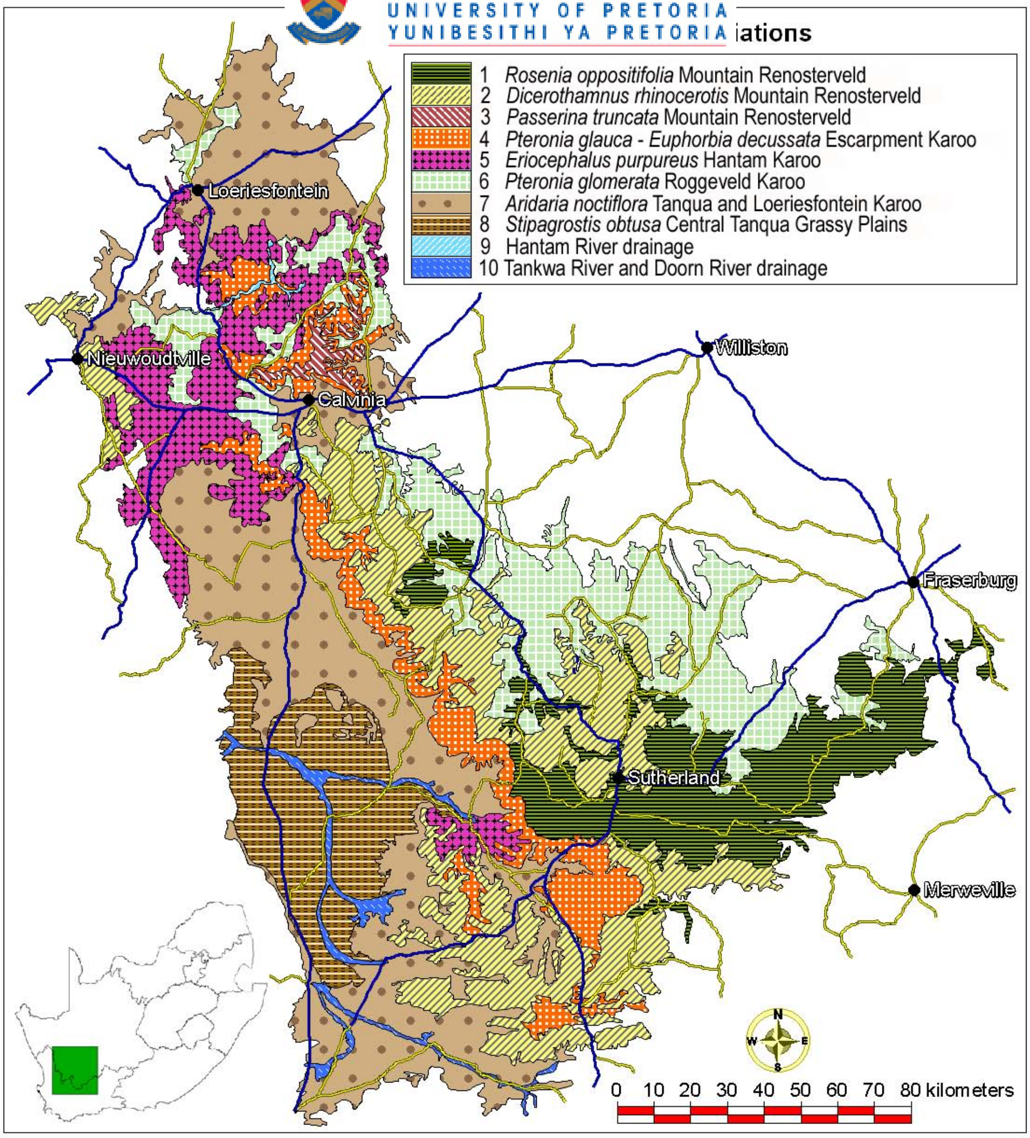

Figure 8.1 The eight plant associations found in the Hantam-Tanqua-Roggeveld subregion (after Van der Merwe et al. 2008a, 2008b).

The vegetation of the Succulent Biome is dominated by dwarf shrubs, many of them being leaf succulents (Werger 1986, Van Rooyen et al. 1990, Rutherford & Westfall 1994, Milton et al. 1997, Mucina et al. 2006). Spectacular autumn and spring floral displays are known to a greater or lesser degree in the Hantam-Tanqua-Roggeveld. A wide range of geophytes (e.g. Iridaceae and Hyacinthaceae), succulents (e.g. Aizoaceae, Crassulaceae and Euphorbiaceae) and annual plants (e.g. Asteraceae, Brassicaceae and Scrophulariaceae) flower on fallow lands but also in the undisturbed natural vegetation (Van Wyk & Smith 2001, Van Rooyen 2002).

The vegetation of the Fynbos Biome is characterised by the co-dominance of usually fine-leaved, sclerophyllous, evergreen shrubs, dwarf shrubs and hemicryptophytes (Rutherford & Westfall 1994). Fynbos, renosterveld and strandveld are the three main vegetation groups of the Fynbos Biome, with only the renosterveld group occurring in the study area. Fynbos vegetation is confined to sandy infertile soils and characterised by the universal presence of restioids, a high cover of ericoid shrubs and the common occurrence of overstorey proteoid shrubs (Cowling et al. 1997). Renosterveld is described as an evergreen, fire-prone shrubland/grassland occurring on relatively fertile clay rich shale and granite derived soils (Boucher & Moll 1981, Cowling et al. 1997).

Three of Acocks's (1953, 1988) veld types are included in the study area namely: Mountain Renosterveld, Succulent Karoo and Western Mountain Karoo. These veld types generally fall into what Low and Rebelo (1996) named the Escarpment Mountain Renosterveld, Lowland Succulent Karoo and Upland Succulent Karoo respectively. The latest vegetation map of South Africa (Mucina et al. 2005, Mucina & Rutherford 2006) identified 12 vegetation types within the area. The eight major plant associations recognised by Van der Merwe et al. (2008a, 2008b) in a recent phytosociological classification and mapping study in the study area form the basis of the present investigation. The eight associations were grouped into three vegetation groups of which two, i.e. the Winter Rainfall Karoo and Tanqua Karoo, form part of the Succulent Karoo Biome and one, i.e. the Mountain Renosterveld, is part of the renosterveld of the Fynbos Biome (Table 8.1).

8.3 Materials and methods

Field surveys were conducted in 2005 using Whittaker's plant diversity plot technique (Shmida 1984) with the methodology described by Shmida (1984) being slightly modified (see Chapter 6 for more detail). The 40 Whittaker sample plots surveyed were selected to cover all eight plant associations distinguished in the area (Van der Merwe et al. 2008a, 2008b) (Figure 8.1). At each site environmental data such as altitude, aspect, slope, position on the slope, geology, topography, percentage stone and stone size, soil type and colour, drainage, erosion, trampling and soil compaction were noted.

All the species encountered in the 1000 m^2 survey plot were noted and a cover value assigned to each species. These species were then classified into broad life form categories following Raunkiaer's (1934) classification as modified by Mueller-Dombois and Ellenberg (1974, see Appendix 1).

The relative contribution of each life form, at a species level and at a vegetation cover level, was calculated for each plot. Comparisons of the life forms were made across the eight plant associations as well as for the three broad vegetation groups (Mountain Renosterveld, Winter Rainfall Karoo and Tanqua Karoo) present in the region. An analysis of variance was performed using the GLM (General Linear Model) Procedure in SAS (SAS® Version 8.2 running on an IBM z9 mainframe computer under z/VM 5.3.0 at the University of Pretoria). The assumption that the variances among treatment levels were constant was violated and thus the data were transformed. A power transformation test indicated that the appropriate transformation would be of the form: $\log_{10}$ (life form + 1). These transformed life form values were then used in the statistical analysis. The complete SAS outputs are included in Appendix 2 for the association level output and Appendix 3 for the vegetation group level output.

Statistical analyses of the data to investigate a degree of succulence were conducted using the STATISTICA computer package (StaSoft, Inc. Version 8, 2300 East 14th Street, Tulsa, OK 74104) (ANOVA's – Kruskal-Wallis test) since the data were not normally distributed.

8.4 Results and discussion

Forty Whittaker plots were surveyed throughout the eight plant associations present in the study area (Table 8.1) (Van der Merwe et al. 2008a, 2008b). A varying number of plots were surveyed in each association due to differences in size and environmental heterogeneity of the associations (Table 8.1). Plant association 1 was co-dominated by cryptophyte, therophyte and chamaephyte species (Table 8.1). A similar dominance structure was found for all other associations of Mountain Renosterveld as well as the associations of the Winter Rainfall Karoo (associations 2, 3, 4, 5 and 6, Table 8.1). The associations in the Tanqua Karoo group had a different dominance structure. Plant association 7 was dominated by chamaephyte species, while association 8 was co-dominated by chamaephyte and cryptophyte species (Table 8.1).

Table 8.1 Mean percentage contribution per life form on a species level in eight plant associations, belonging to three broad vegetation groups, in the Hantam-Tanqua-Roggeveld subregion. The mean number of species per life form is indicated in brackets

Plant association		Broad vegetation group	No. of plots	Mean percentage contribution by species (Mean number of species per life form)						
				P	Ch	H	C	T	L	Par
1	*Rosenia oppositifolia* Mountain Renosterveld	Mountain Renosterveld	5	3.0 (2.2) abc	24.7 (19.0) a	10.7 (8.4) ab	33.2 (25.6) b	27.0 (20.4) c	1.2 (1.0) ab	0.2 (0.2) a
2	*Dicerothamnus rhinocerotis* Mountain Renosterveld	Mountain Renosterveld	10	5.4 (4.0) c	26.3 (20.4) a	8.2 (6.3) ab	30.6 (23.9) b	26.8 (20.9) c	2.5 (1.9) c	0.3 (0.2) a
3	*Passerina truncata* Mountain Renosterveld	Mountain Renosterveld	2	3.5 (3.0) abc	34.6 (31.0) a	7.7 (7.0) ab	27.0 (24.5) b	26.1 (23.0) c	1.1 (1.0) abc	0.0 (0.0) a
4	*Pteronia glauca – Euphorbia decussata* Escarpment Karoo	Winter Rainfall Karoo	4	6.1 (5.3) c	34.6 (27.8) a	8.1 (7.0) ab	25.4 (21.5) b	22.3 (18.0) c	3.5 (3.0) c	0.0 (0.0) a

Table 8.1 (continued)

5	*Eriocephalus purpureus* Hantam Karoo	Winter Rainfall Karoo	9	1.8 (1.2) ab	29.7 (19.0) a	7.1 (4.2) a	27.3 (16.7) b	32.0 (18.6) c	2.2 (1.3) bc	0.0 (0.0) a
6	*Pteronia glomerata* Roggeveld Karoo	Winter Rainfall Karoo	3	1.1 (0.7) a	30.4 (15.0) a	10.6 (5.3) ab	24.9 (14.3) b	31.4 (16.0) c	1.6 (1.0) abc	0.0 (0.0) a
7	*Aridaria noctiflora* Tanqua and Loeriesfontein Karoo	Tanqua Karoo	4	3.7 (0.8) abc	47.6 (10.3) a	13.9 (3.3) b	18.2 (5.0) a	15.6 (4.3) b	1.0 (0.3) a	0.0 (0.0) a
8	*Stipagrostis obtusa* Central Tanqua Grassy Plains	Tanqua Karoo	3	3.7 (0.3) ab	39.0 (4.3) a	14.0 (1.7) ab	32.4 (4.0) b	4.8 (0.7) a	6.1 (0.7) c	0.0 (0.0) a

P = phanerophyte, Ch = chamaephyte, H = hemicryptophyte, C = cryptophyte, T = therophyte, L = liana and Par = parasite. Within a column, values with the same letters do not differ significantly at $\alpha = 0.05$. Letters should only be compared within a life form.

An analysis of variance using the GLM (General Linear Model) Procedure in SAS on the transformed data indicated that the interaction between the main factors was significant and thus the interpretation of the results has to done on the interaction level (Table 8.2).

Table 8.2 Summary output of the analysis of variance (GLM) with association and life form (species level) as main factors

Source of variation	Degrees of freedom	Sum of squares	Mean square	F value	P value
Association	7	0.8205	0.1172	2.31	0.0273
Life form (species level)	6	58.1393	9.6899	190.83	< 0.0001
Association x Life form (species level)	42	6.4168	0.1528	3.01	< 0.0001

The total number of species per life form encountered in the 1000 m² Whittaker plots expressed as a percentage of the total number of species indicated that the contributions of phanerophyte species were low (1.1 – 6.1%) with a significant difference ($p < 0.01$ in all instances) found between associations 2 and 4 and associations 5, 6 and 8. In contrast, contributions by chamaephyte species were generally high (24.7 – 47.6%) with no significant difference found between them at an association level. The higher number of chamaephyte species found relative to phanerophyte species in this study could be a case of the succulent species mostly being found among the chamaephyte life form. Hemicryptophyte species' contributions were similar yet produced a significant difference between association 5 and association 7 ($p < 0.05$).

Contributions by cryptophyte (geophyte) species were relatively constant throughout and ranged from 18.2% to 33.2%. These high values confirm the high diversity of bulbous plants in both the Fynbos, especially renosterveld, and Succulent Karoo which is a striking feature shared by these two areas (Esler et al. 1999a, Procheş et al. 2005, 2006). Association 7 was marked by a lower cryptophyte contribution which was found significantly different ($p < 0.05$) from all other associations. It should be noted however, that the data used in this study were collected in 2005, which was a very poor rainfall year. This is expected to have had a marked effect on the number of geophyte and annual species encountered and their contributions to the flora could have been underestimated.

Therophyte (annual) contributions were lowest in the two associations from the Tanqua Karoo and differed significantly ($p < 0.05$) between association 7 and all other associations as well as between association 8 and all other associations. In general, therophyte dominance indicates the desert nature of the climate in a study area (Withrow 1932, Raunkiaer 1934, Van Rooyen et al. 1990, Fox 1992, Van Rooyen 1999). It is therefore surprising that the therophytes made a significantly smaller contribution in the two Tanqua Karoo associations (associations 7 and 8) which are located in the most arid part of the study area but this is probably a result of the below normal rainfall of the survey year. It has been suggested that in desert and semi-desert areas a relatively predictable seasonal rainfall favours the development of a therophyte flora (Westoby 1980, Cowling & Pierce 1999). Therophytes are believed to be more resistant to summer drought than the hemicryptophytes and geophytes, since the former spend the summer in the form of seeds and the latter in the form of vegetative organs (Danin & Orshan 1990). Raunkiaer (1934) suggested that the biological spectra of Mediterranean-type regions are also characterised by high percentages of therophytes that survive the dry summer in the form of seeds (Danin & Orshan 1990). However, life form spectra with a relatively low percentage of therophytes are known from Mediterranean climates e.g. South Australia and South Africa.

Liana species were present in low numbers in all the plant associations however, a significant difference was found for lianas between association 1 and associations 2, 4 and 8 as well as between association 7 and associations 2, 4, 5 and 8 ($p < 0.05$). Parasite species were only encountered in plant associations 1 and 2 (Table 8.1).

The GLM Procedure on the transformed life form (species level) and vegetation group data also produced a significant difference at the interaction level (Table 8.3). At the species level, the phanerophyte contribution was significantly lower ($p < 0.05$) in the Winter Rainfall Karoo and Tanqua Karoo groups than in the Mountain Renosterveld group. Hemicryptophytes made a significantly smaller ($p < 0.05$) contribution in the Winter Rainfall Karoo than in the Tanqua Karoo, whereas the cryptophyte contribution was significantly ($p < 0.05$) higher for the Mountain Renosterveld than for the Tanqua Karoo. Therophytes contributed significantly ($p < 0.0001$) less in the Tanqua Karoo group than in both the Mountain Renosterveld and Winter

Rainfall Karoo groups. No significant difference was found at the vegetation group level for chamaephytes, lianas or parasites.

Table 8.3 Summary output of the analysis of variance (GLM) with vegetation group and life form (species level) as main factors

Source of variation	Degrees of freedom	Sum of squares	Mean square	F value	P value
Vegetation group	2	0.5706	0.2853	5.15	0.0064
Life form (species level)	6	62.1143	10.3524	187.05	< 0.0001
Vegetation group x Life form (species level)	12	3.7066	0.3089	5.58	< 0.0001

The contribution of each life form to the vegetation cover in the various plant associations (Table 8.4) produced different results to those found at a species level (Table 8.1) and once again the statistical analysis indicated a significant interaction between the life forms and associations (Table 8.5).

Table 8.4 Mean percentage cover contribution per life form in eight plant associations, belonging to the three broad vegetation groups, in the Hantam-Tanqua-Roggeveld subregion. The mean cover per life form is indicated in brackets

Plant association		**Broad vegetation group**	**No. of plots**	**Mean percentage contribution by cover (Mean cover per life form)**						
				P	Ch	H	C	T	L	Par
1	*Rosenia oppositifolia* Mountain Renosterveld	Mountain Renosterveld	5	16.6 (18.4) cd	47.1 (53.1) abc	3.5 (3.9) a	14.7 (16.5) a	17.8 (20.0) ab	0.3 (0.3) a	0.1 (0.1) a
2	*Dicerothamnus rhinocerotis* Mountain Renosterveld	Mountain Renosterveld	10	30.8 (33.1) de	33.9 (34.7) ab	2.91 (3.2) a	18.2 (21.7) a	13.3 (14.5) ab	0.8 (0.9) a	0.1 (0.1) a
3	*Passerina truncata* Mountain Renosterveld	Mountain Renosterveld	2	38.3 (38.0) e	32.1 (30.5) abc	3.7 (3.5) a	11.8 (11.3) a	13.6 (13.1) ab	0.5 (0.5) a	0.0 (0.0) a
4	*Pteronia glauca – Euphorbia decussata* Escarpment Karoo	Winter Rainfall Karoo	4	37.1 (42.1) e	40.0 (43.2) abc	3.3 (3.7) a	9.4 (10.3) a	8.8 (9.8) a	1.3 (1.4) a	0.0 (0.0) a
5	*Eriocephalus purpureus* Hantam Karoo	Winter Rainfall Karoo	9	0.9 (0.9) a	51.4 (48.1) a	2.5 (2.5) a	8.3 (8.2) a	36.5 (40.9) b	0.5 (0.4) a	0.0 (0.0) a

Table 8.4 (continued)

6	*Pteronia glomerata* Roggeveld Karoo	Winter Rainfall Karoo	3	0.3 (0.2) ab	49.2 (51.3) c	2.9 (1.4) a	11.5 (6.2) a	12.3 (8.3) ab	0.5 (0.4) a	0.0 (0.0) a
7	*Aridaria noctiflora* Tanqua and Loeriesfontein Karoo	Tanqua Karoo	4	1.2 (0.3) ab	79.0 (38.0) c	12.5 (5.9) a	3.8 (2.1) a	3.6 (2.1) ab	0.3 (0.0) a	0.0 (0.0) a
8	*Stipagrostis obtusa* Central Tanqua Grassy Plains	Tanqua Karoo	3	0.1 (0.0) abc	25.7 (11.6) c	71.2 (53.5) a	2.4 (1.5) a	0.5 (0.3) ab	0.1 (0.1) a	0.0 (0.0) A

P = phanerophyte, Ch = chamaephyte, H = hemicryptophyte, C = cryptophyte, T = therophyte, L = liana and Par = parasite. Within a column, values with the same letters do not differ significantly at α = 0.05. Letters should only be compared within a life form.

Phanerophytes made a significantly larger contribution to the vegetation cover of associations 1 to 4 than in associations 5 to 8 ($p < 0.05$), with a significant difference ($p < 0.05$) between association 1 and associations 3 and 4 also found. Chamaephytes were abundant in all the associations but their contribution to the vegetation cover varied greatly. A significant difference in chamaephyte cover was found between associations 2 and 5 and associations 6, 7 and 8 ($p < 0.05$).

Hemicryptophytes, lianas and parasites contributed the least to the vegetation cover in all the associations except for association 8 where the hemicryptophyte cover, as a result of the dominance and high cover of the grass *Stipagrostis obtusa*, was higher than in all other associations yet no significant differences were found. The cryptophytes' contribution to the vegetation cover varied from 2.4% to 18.2% with no significant differences found. On a therophyte cover level the only significant difference ($p < 0.05$) was found between association 4 and association 5.

Table 8.5 Summary output of the analysis of variance (GLM) with association and life form (cover level) as main factors

Source of variation	Degrees of freedom	Sum of squares	Mean square	F value	P value
Association	7	1.7944	0.2563	3.69	0.0009
Life form (cover level)	6	61.7956	10.2992	148.26	< 0.0001
Association x Life form (cover level)	42	11.8453	0.2820	4.06	< 0.0001

The interaction between the life forms (cover level) and vegetation groups also produced a significant difference (Table 8.6) and thus this interaction is used to further interpret the cover level data. Chamaephyte cover was found to be significantly lower ($p < 0.05$) in the Tanqua Karoo than in the Mountain Renosterveld and Winter Rainfall Karoo. Phanerophyte cover was found to be significantly higher ($p < 0.0001$) in the Mountain Renosterveld than the Winter Rainfall Karoo as well as significantly higher ($p < 0.05$) in these two groups than the Tanqua Karoo. No significant differences were found for the hemicryptophyte, cryptophyte, therophyte, liana or parasite life forms at the cover level.

Table 8.6 Summary output of the analysis of variance (GLM) with vegetation group and life form (cover level) as main factors

Source of variation	Degrees of freedom	Sum of squares	Mean square	F value	P value
Vegetation group	2	1.0385	0.5192	6.08	0.0026
Life form (cover level)	6	68.7823	11.4637	134.16	< 0.0001
Vegetation group x Life form (cover level)	12	6.0313	0.5026	5.88	< 0.0001

Because of the controversy as to whether the vegetation in the study area falls within the Succulent Karoo or the Fynbos Biomes, a degree of succulence was calculated from the data at a species as well as vegetation cover level. It was found that succulence usually occurred among the chamaephyte, hemicryptophyte and therophyte species for associations 1 to 8, however, for association 4, one phanerophyte species, *Tylecodon paniculata*, fell within the succulent category in two of the surveyed plots.

At a species level the succulent species' percentage contribution to the Mountain Renosterveld was very low and ranged from 2.9% to 4.1% among the associations, with the percentage contribution to the Winter Rainfall Karoo higher at 13.5 to 16.9%, while the percentage contribution to the Tanqua Karoo was highest at 30.3 and 31.1% (Figure 8.2). Statistically (Kruskal-Wallis test), Winter Rainfall Karoo and Tanqua Karoo succulent species contributions were significantly higher than Mountain Renosterveld species contributions ($p < 0.05$).

Succulent species' cover ranged from 1.4% to 58.2% throughout the study area (Figure 8.3). Values for the Mountain Renosterveld ranged from 1.4% (association 2) to 3.5% (association 3) and 11.6% (association 1) even although the contributions of succulents to the species level analysis in these three associations were similar (Figure 8.2). The contribution of succulents to the vegetation cover in the Winter Rainfall Karoo vegetation group also varied greatly from 28.8% in association 4, 35.4% in association 5 and was lowest for association 6 with only 9.1%. The 'true' succulent vygieveld of the Tanqua Karoo (association 7) had a high succulent cover of 58.2%, while the grassy plains (association 8) had a lower succulent cover contribution of 32.6%. Although the percentage cover contribution between associations 7 and 8 differed greatly, the percentage contribution by species was very similar (Figure 8.2). An ANOVA (Kruskal-Wallis test) comparing the succulent life form between the eight plant associations found a significant difference ($p < 0.05$) between the associations, as well as a significant difference between the three broad vegetation groups where the Mountain Renosterveld vegetation group was found to be significantly different from the other two vegetation groups ($p < 0.001$).

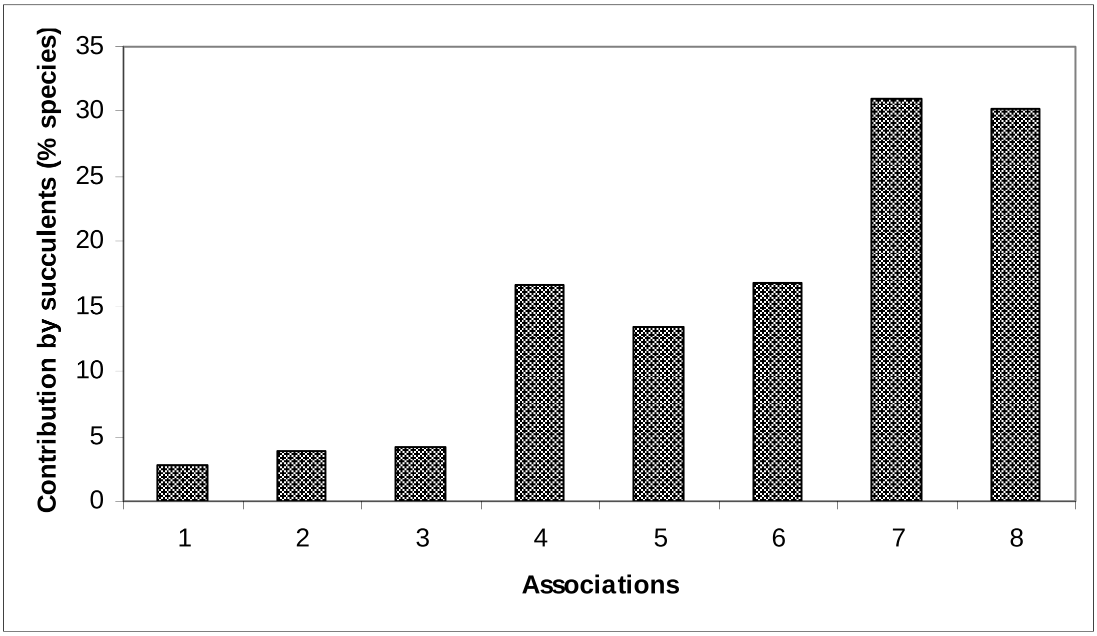

Figure 8.2 Number of succulent species expressed as a percentage of the total number of species in eight plant associations in the Hantam-Tanqua-Roggeveld subregion.

The classification of plants and vegetation into major types on the basis of plant form is based on the observation that the capacity to survive different geographic, climatic and ecological conditions is often linked to plant architecture and physiognomy (Vandvik & Birks 2002). Succulence is a determining factor for defining the Succulent Karoo Biome with regression models indicating that rainfall evenness is an important factor explaining succulent richness per site (Cowling et al. 1994). Thus, centres of succulent diversity occur outside the strongly winter rainfall zones (Cowling et al. 1994). A number of environmental variables have been found to be correlated to succulence. According to Werger (1986) succulents are common in the winter rainfall area, where night frosts below -4°C are rare. The incidence of succulence is also correlated with soil salinity (Barkman 1979) and possibly with levels of soil phosphorus, potassium, calcium and magnesium (Hoffman & Cowling 1987).

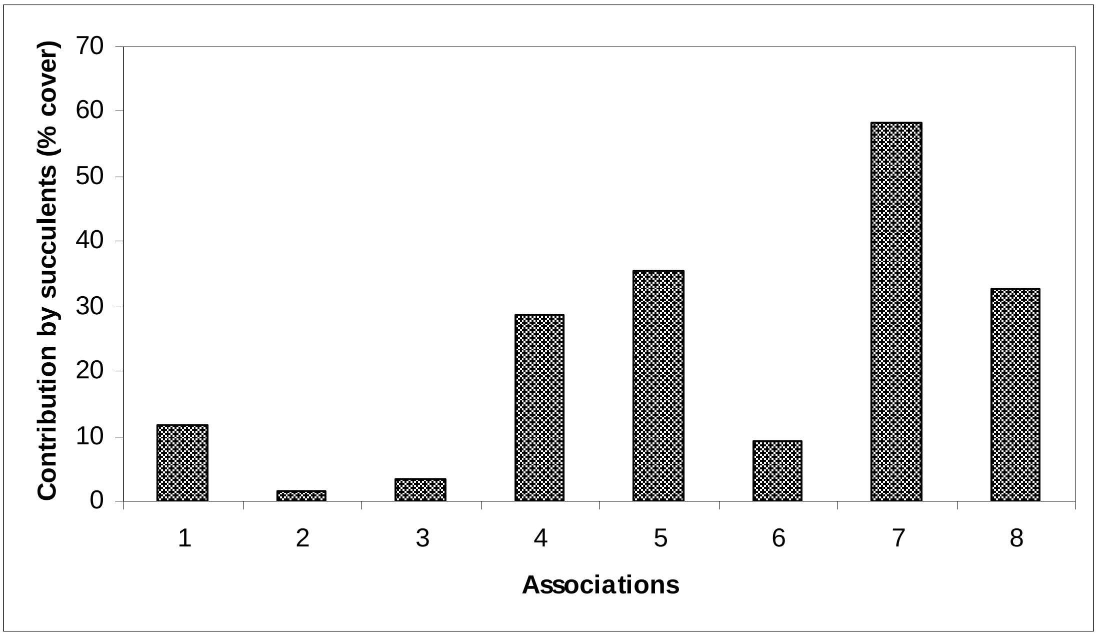

Figure 8.3 Percentage succulent vegetation cover expressed as a percentage of the total vegetation cover in eight plant associations in the Hantam-Tanqua-Roggeveld subregion.

The data collected in this study highlights the importance of the succulent life form relative to the other life forms at a species level as well as at a vegetation cover level. At a species level there was a clear difference between values for the Mountain Renosterveld (lowest), Winter Rainfall Karoo (intermediate) and Tanqua Karoo (highest). However, at a vegetation cover level, this was not as clear, with Mountain Renosterveld values low and Tanqua Karoo values high but Winter Rainfall Karoo values straddling these two extremes. The high succulent and species cover levels for the Tanqua Karoo confirm the statement by Cowling et al. (1994) that centres of succulent diversity occur outside the strongly winter rainfall zones.

The low presence of the succulent life form in the Mountain Renosterveld vegetation group at a species and vegetation cover level and high cover contribution of phanerophytes re-enforces the delineation by Mucina and Rutherford (2006) and Van der Merwe et al. (2008a) who place this vegetation type within the Fynbos Biome and not the Succulent Karoo Biome. However, the succulent life form percentage vegetation cover contribution of plant association 1, with a value of 12.5%, is higher than what would be expected for Mountain Renosterveld vegetation indicating that the escarpment types of renosterveld show strong karroid affiliations (Mucina & Rutherford 2006). This association (*Rosenia oppositifolia* Mountain Renosterveld) was also the association that showed some floristic links between the Fynbos Biome related vegetation and Succulent Karoo Biome related vegetation in the Hantam-Tanqua-Roggeveld area (Van der Merwe et al. 2008a, 2008b). The presence of such transitional units re-enforces various authors' contentions that there is a relationship between the Karoo and Cape Flora (Bayer 1984, Gibbs Russell 1987, Jürgens 1997) and supports Jürgens (1997) who proposed the recognition of the Floristic Kingdom of the Greater Cape Flora including at least two separate regions, the Cape Floristic Region and the Succulent Karoo Region. This concept was recently supported by Born et al. (2007), who investigated an area named the Greater Cape Floristic Region.

In this study, the percentage contribution of succulent species to the Winter Rainfall Karoo was intermediate to the values found for the Mountain Renosterveld and Tanqua Karoo. However, succulent vegetation cover for associations 4 and 5 was significantly higher than for association 6. This could be as a result of association 6 (Roggeveld Karoo) having a strong transitional nature as it is located between the Mountain Renosterveld vegetation of the Roggeveld Mountains and the summer rainfall Nama Karoo Biome, with boundaries between the Succulent and Nama Karoo fluid and blurred (Milton et al. 1997). The low cover of succulents in association 6 (Roggeveld Karoo) supports the view of Rutherford and Westfall (1994) who incorporated the area in the Nama Karoo Biome. A high percentage contribution of succulent species was encountered in the Tanqua Karoo, yet the succulent contribution to the vegetation cover was much higher in association 7 than in association 8. The larger contribution by succulent species to the life form spectra at a species and vegetation cover level in the Winter Rainfall Karoo and Tanqua Karoo than in the Mountain Renosterveld confirms that the former two vegetation groups belong within the Succulent Karoo Biome.

Overall there is a clear difference between the life form spectra of the different broad vegetation groups with the Mountain Renosterveld of the Fynbos Biome differing most from the Tanqua Karoo, a strong Succulent Karoo part of the Succulent Karoo Biome. However, such spectra differ depending on whether only the presence of species is taken into account or also their cover or other quantitative vegetational parameters.

A comparison of the life form spectra found in the Hantam-Tanqua-Roggeveld subregion with another site in the Succulent Karoo (Goegap Nature Reserve), the winter rainfall Mojave Desert and a site in the Fynbos Biome (Swartboskloof) is presented in Table 8.7. The patterns found between associations 1 to 8 and Goegap Nature Reserve are more similar than the pattern found in the Mojave Desert. In general, the hemicryptophyte percentage was higher and the cryptophyte percentage was lower at the Goegap Nature Reserve than in the study area. None of the Mountain Renosterveld life form spectra (associations 1 to 3) compared well with the Fynbos Biome spectrum at Swartboskloof, where the phanerophyte contribution was much higher and therophyte contribution much lower than in the study area. This is supported by Oliver et al. (1983, in Rutherford & Westfall 1994) who state that the vegetation of the Roggeveld is only marginally similar to the vegetation structure of the Fynbos Biome but that it shows some floristic affinities to the Fynbos Biome.

Table 8.7 A comparison of life form spectra between the eight plant associations (Assoc. 1-8) in the study area, Goegap Nature Reserve (Succulent Karoo), Mojave Desert (Desert) and Swartboskloof (Fynbos Biome)

Vegetation	Life forms					
	Phanerophyte	Chamaephyte	Hemicryptophyte	Cryptophyte	Therophyte	Other
Assoc. 1	3.0	24.7	10.7	33.2	27.0	4
Assoc. 2	5.4	26.3	8.2	30.6	26.8	2.8
Assoc. 3	3.5	34.6	7.7	27.0	26.1	1.1
Assoc. 4	6.1	34.6	8.1	25.4	22.2	3.5
Assoc. 5	1.8	29.7	7.1	27.3	32.0	2.2
Assoc. 6	1.1	30.4	10.6	24.9	31.4	1.6
Assoc. 7	3.7	47.6	13.9	18.2	15.6	1.0
Assoc. 8	3.7	39.0	14.0	32.4	4.8	6.0
Goegap Nature Reserve	6.0	32.0	17.0	17.0	28.0	0.0
Mojave desert	11.3	6.0	50.0	0.7	32.0	0.0
Swartboskloof	34.0	31.0	16.0	15.0	4.0	0.0

Data extracted from Beatley (1976) (in Esler et al. 1999b) and Van Rooyen et al. (1990).

8.5 Conclusions

A comparison of various life forms in the eight plant associations identified in the Hantam-Tanqua-Roggeveld subregion (Van der Merwe et al. 2008a, 2008b) produced different results when considered at a species level or at a vegetation cover level. Additionally, patterns between the three broad vegetation groups of the Mountain Renosterveld, Winter Rainfall Karoo and Tanqua Karoo differed at the different levels.

Six of the eight associations (Mountain Renosterveld and Winter Rainfall Karoo associations) were dominated by chamaephyte, cryptophyte (geophyte) and therophyte species with one association (Tanqua Karoo) dominated by only chamaephyte species and another association (Tanqua Karoo) by chamaephyte and cryptophyte species. Phanerophyte species contributions were low and a significantly higher contribution was found in the Mountain Renosterveld than both the Winter Rainfall Karoo and Tanqua Karoo. Chamaephyte species contributions were generally high and no significant differences were found between the three vegetation groups. Hemicryptophyte contributions were significantly smaller in the Winter Rainfall Karoo than the Tanqua Karoo. Cryptophyte species contributions were relatively constant across the three vegetation groups but were significantly higher for the Mountain Renosterveld than the Tanqua Karoo. Therophyte contributions were similar in the Mountain Renosterveld and Winter Rainfall Karoo and significantly less in the Tanqua Karoo. No significant differences were found at the vegetation group level for lianas or parasites.

On a vegetation cover level, phanerophyte contributions were found to be significantly higher in the Mountain Renosterveld than the Winter Rainfall Karoo as well as significantly higher between these two groups and the Tanqua Karoo. Chamaephyte cover varied greatly but was significantly higher in the Mountain Renosterveld and Winter Rainfall Karoo groups than in the Tanqua Karoo vegetation group. No significant differences were found for hemicryptophytes, cryptophytes, therophytes, lianas and parasites at the cover level.

The Succulent Karoo Biome is largely defined by the presence of succulents and thus this trait was extracted from the life form categories. Most of the succulent species were found to originate from the chamaephyte, hemicryptophyte and therophyte species and one species, was a phanerophyte. Succulent cover was generally lowest for the Mountain Renosterveld, with higher cover values found in the Winter Rainfall Karoo and the Tanqua Karoo. This confirms the Succulent Karoo Biome affinities of the Winter Rainfall Karoo and Tanqua Karoo. Yet, a higher than expected vegetation cover of the succulent life form was found for association 1, which is a strong Mountain Renosterveld (Fynbos Biome) vegetation group, indicating its transitional nature between the two biomes.

A comparison of life form spectra with another site in the Succulent Karoo produced similar patterns, however, these patterns are very different from the pattern encountered in the winter rainfall Mojave Desert. The Mountain Renosterveld life form spectra determined in this study did not compare well with a Fynbos Biome site where phanerophyte contribution was much higher and therophyte contribution much lower.

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