

Ecological studies on the vegetation of a semi-arid desert  
following a climatic gradient (Richtersveld, South Africa)

Inaugural Dissertation

zur

Erlangung des Doktorgrades

der Mathematisch-Naturwissenschaftlichen Fakultät

der Universität zu Köln

vorgelegt von

Stefanie Nußbaum

aus Köln

Köln 2003

Berichtersteller:

Prof. Dr. Michael Melkonian

PD Dr. Christoph Wallossek

Prof. Dr. Reinhard Bornkamm

Tag der letzten mündlichen Prüfung: 3. Juli 2003

## **Acknowledgments**

I was lucky enough to experience the great South African hospitality on every trip during the last years. In particular I would like to take this opportunity to thank: Jill and Peddy Gordon, The Moses Family, Mike and Jackie Solomon, Ashia Petersen, Annelise Le Roux, Hanny Pool and The Bezuidenhout family. Thank you also to Mike Solomon for organising an office for me in Brandkaros.

I am also extremely grateful to the staff of the South African National Parks for their extensive cooperation and inexhaustible support and words of encouragement. Hugo Bezuidenhout needs to be thanked for his tireless patience and his belief in my work and its success. Peddy Gordon, with whom I share a love of the Richterveld, has become a good friend over the years. Howard Hendrick's enthusiastic stories of the country and its people transported me into another world during evening meals and Rooibosch tea.

I would like to thank the workers of the National Botanical Institute, Cape Town for the stimulating scholarly discussions. Tim Hoffman and his colleagues were always prepared to help with any logistical problems. Further, I would like to acknowledge Pascale Cheselet for her help with the identification of the Mesembs.

I am indebted to Annelise le Roux, Nature Conservation, Stellenbosch for being able to view her large collection of Namaqualand species and for her enormous scientific support.

I would also like to show my appreciation to the Nature Conservation, Northern Cape, for the issue of a collecting and export permit.

Thanks also Eileen Küpper who proof-read this text and applied the finishing touches to my English. She worked hard day and night. Thanks a lot.

## **Danksagung**

Ein außerordentlicher Dank gilt Herrn Prof. Dr. M. Melkonian, Herrn Priv. Doz. Dr. C. Wallossek und Herrn Prof. Dr. R. Bornkamm für die Betreuung meiner Arbeit.

Ein Dank geht an Herrn Prof. Dr. N. Jürgens, der durch sein Engagement und seine Begeisterung für aride Gebiete mein Interesse an dieser Arbeit geweckt hat. Ihm verdanke ich die Einführung in das Untersuchungsgebiet und viele Anregungen, die dieser Arbeit zu Grunde liegen.

Ohne die Bereitstellung finanzieller Mittel in den ersten Jahren meiner Arbeit wären die mehrmonatigen Forschungsreisen nach Südafrika nicht möglich gewesen. Hierfür möchte ich mich besonders bedanken bei der Schimper-Stiftung, der Merensky-Stiftung, der Johanna und Fritz Buch-Gedächtnis-Stiftung und nicht zuletzt bei meinen Eltern.

In den Jahren 1996 und 1997 unterstützte die Graduiertenstiftung des Landes Nordrhein-Westfalen mein Projekt. Ihr gilt ein großer Dank.

Die Assoziation meines Projektes an den Sonderforschungsbereich 389 „Kultur- und Landschaftswandel im ariden Afrika“ (ACACIA) der Deutschen Forschungsgemeinschaft brachte mir wertvolle wissenschaftliche Anregungen aber auch viele logistische Vorteile. All jenen sei gedankt, die diese Zusammenarbeit ermöglichten.

Den Mitarbeitern des Teilprojektes E1 mit dem Thema ‚GIS-gestützter Atlas holozäner Nutzungspotentiale ausgewählter Arbeitsgebiete‘ des Sonderforschungsbereichs ACACIA, vor allem Frank Darius und Andreas Bolten danke ich für die Bereitstellung von Hard- und Software und die technische Unterstützung bei der Erstellung der Karten, Höhen- und Klimamodelle.

Bei Michael Facklam (Bodenkunde, TU Berlin) möchte ich mich für die Bodenartbestimmung herzlich bedanken.

Große Unterstützung und Beistand erfuhr ich durch die Mitarbeiter des Botanischen Instituts Köln. Insbesondere danke ich Rosemarie Schäferhoff, Helga Tiebel, Dr. Karl-Heinz Linne von Berg und Hans Zimmer.

Herbert und Magdalene Kersberg danke ich für ihr Interesse an meiner Arbeit und für eine schöne Zeit im Richtersveld. Der langjährigen Erfahrung wissenschaftlicher Arbeit in Afrika von Herrn Prof. Dr. H. Kersberg verdanke ich wertvolle Ideen für meine Arbeit.

Meinen Kolleginnen und Kollegen des Heinrich-Barth-Institutes Köln spreche ich meinen Dank aus für ihre Geduld und Nachsicht, mit der sie den Fortgang meiner Arbeit verfolgt haben.

Meinen Weggefährtinnen Inge Gotzmann und Anja Linstädter danke ich für intensive Kooperation und wissenschaftlichen Austausch, aber vor allem für ihre Freundschaft, die so manche schwere Stunde durch Stärke und Ausdauer überstanden hat.

Meine Freunde haben mich durch diese Zeit getragen. Ohne ihre moralische Unterstützung und praktische Hilfe hätte ich diese Arbeit wohl nicht zuende gebracht. Vielen Dank.

Meiner Familie, besonders meinen Eltern, Frank, Josefine und Luise danke ich für ihren lieben Beistand und ihre Sorge um mein Wohl.

## Table of contents

### 1 Introduction 5

- 1.1 Aim of the study 8
- 1.2 Physical environment 8
  - 1.2.1 Geography and landscape units 8
  - 1.2.2 Geology 15
  - 1.2.3 Soils 19
  - 1.2.4 Climate 20
- 1.3 Biotic setting 22
  - 1.3.1 Flora and vegetation 22
  - 1.3.2 Present and former land use – history of the Richtersveld National Park 28

### 2 Methods 33

- 2.1 Sampling procedure 33
- 2.2 Plant identification, taxonomy and nomenclature 35
- 2.3 Chemical and physical soil analysis 38
- 2.4 Derivation of additional explanatory variables 39
  - 2.4.1 Satellite remote sensing data sets 39
  - 2.4.2 Climatic parameters 40
- 2.5 Classification and ordination of the vegetation data 40
- 2.6 Vegetation mapping 48

### 3 Results 49

- 3.1 Classification 49
  - 3.1.1 Cluster analysis 49
  - 3.1.2 Braun-Blanquet approach 52
- 3.2 Ordination 94
  - 3.2.1 Data set of all 230 classified relevés 94
  - 3.2.2 Data set of 251 relevés with soil properties only 96
  - 3.2.3 Data set of 251 relevés with all environmental variables 100
  - 3.2.4 Data set of the coastal plain habitats 102
  - 3.2.5 Data set of the slope habitats 103
  - 3.2.6 Data set of the Succulent Karoo slope habitats 106
  - 3.2.7 Data set of the Nama Karoo slope habitats 108
  - 3.2.8 Data set of the flood plains and drainage lines 109
  - 3.2.9 Selected species – environment correlations 110

**4 Discussion 121**

- 4.1 Environmental control of the spatial vegetation patterns 121
- 4.2 Classification of the northern Richtersveld vegetation - problems and comparison 125
- 4.3 Life form spectra of the northern Richtersveld vegetation - comparison with other deserts 137
- 4.4 Digression: Reflections on degradation and the conflict of land use in the Richtersveld 143

**5. Conclusion 151**

**6. References 155**

**7. Index 171**

**8. Appendix 177**

## 1. Introduction

The Richtersveld is situated in the most arid region of South Africa and can be interpreted as the southerly part of the Namib Desert (Koch 1962). This semi-desert, with a precipitation well below 150 mm per year, is unexpectedly rich in plant and animal life correlated with a high diversity in terms of climate and geology. This unusual biodiversity, with a high rate of endemism, is the result of a large supply of different habitats, and is also a product of a long floristic history. The border of two floristic kingdoms, *Greater Cape Flora* and *Palaeotropis* is located within the Richtersveld (Jürgens 1991). It is expressed by a transition from a succulent dominated dwarf shrub-land on the western coast to a more open scrubland, with increasing grass cover, to the east.



Due to these exceptional features a national park was established in 1991 in the most diverse part of this area, where the traditional semi-nomadic life-style still exists. The migration of the livestock is orientated to the seasonal shifting of the precipitation patterns. During the dry summer, with occasional thunderstorms, the small stock herders make use of the grazing along the Orange River, while moving to the foothills of the mountains in winter where the animals gain enough water from the succulent vegetation.

The whole Richtersveld is characterised by high and steep mountain ranges, which together, with the rare water source, limit the size of the human population (c. 3000 inhabitants). The southern and rather flat western part of the Richtersveld is communally owned and used for extensive livestock production.

In spite of its limited exploitation potential, in terms of water resource and high relief energy, the Richtersveld is the focus for a serious conflict of interests. The whole region is rich in mineral resources; in particular diamonds and copper are mined in this region. The mining companies along the coast and the Orange River banks use and destroy valuable land which might otherwise be used as productive pastures for stock farmers and, in accordance with a landscape of exceptional beauty, attractive for tourists visiting the national park.

There also exists a conflict between the traditional semi-nomadic economy of the *Nama* people, who need extended space for migration processes, and the more sedentary economy which uses the land for extensive livestock production (Berzborn 2002). This kind of exploitation is mostly combined with the fencing in of land. Even within the younger *Nama* herders a change of moral concept appears. The flock increasingly becomes an object of prestige, displaying the owner's wealth. This aspect leads to an increasing number of animals per stock (pers. comm. H. Hendricks 1997).

Thanks to the management of the Richtersveld Park the number of tourist per year has increased. The construction of sanitary facilities within the park at already existing campsites is planned, to make the park more attractive to visitors (pers. comm. of the park co-ordinator Mr Giel de Kock 2003).

The increasing scientific research in the Richtersveld has uncovered the importance of protecting its biodiversity and diverse landscape beyond the park boundaries.

Recently the diamond mines along the coast have increasingly shown decreased profits so that their closure is expected within the next ten years (Solomon 1997). Whilst the mining activities are seen to be critical on the basis of landscape destruction, these companies have, on the other hand, an important economical value for the herder families as the only source of cash income (Mussgnug 1995). More than half of the herder families have one or two relatives working in the mining companies. The closure of the mines means the loss of employment for many people. Despite this dependence on the mines, the pastoralist tradition has never died out. This strong link to the land could lead to a return of the unemployed mine workers to the traditional forms of pastoralism (Solomon 1997). Therefore the pressure on the land will increase, which could prove disastrous for the ecology of this area. Through over grazing and the inevitable consequence of increasing desertification, it could provide a devastating setback to stock farming potential (Solomon 1997). With the closure of the mines a different economic sector will gain importance: tourism.



All these exploitation interests influence and, in future, will increasingly influence the ecosystem and therefore the vegetation cover. In some locations an over-use with the resulting degradation is obvious. In this context there is an urgent need for scientific research to document the present state of the ecosystem.

Furthermore, a process of negotiation is necessary between all the participants due to the apparent irreconcilability between the most important forms of land use such as pastoralism, mining and conservation. The management committee of the Richtersveld National Park together with the local communities and the mining companies have taken up these problems in order to work out a sustainable concept for the future. The Richtersveld National Park represents a totally new approach to nature conservation in South Africa owing to the fact that it is the first fully contractual national park in South Africa, managed by a committee on which elected representatives of the local people serve in co-operation with members of the National Parks Board. It is therefore an important role model for a new approach to conservation that is certain to become increasingly widespread in South Africa (SANP 1996).

The aim of the Richtersveld management plan is to combine the maintenance of the traditional life-style and culture of the *Nama* people together with associated forms of sustainable land use and the conservation of the landscape in an unspoilt condition, thus maintaining its great biodiversity. The main function of this research is to promote the attainment of these conservation objectives. The main research tasks are named *inter alia* (SANP 1996):

- Inventories of plants and vertebrates species diversity
- Vegetation description and mapping
- Monitoring of the dynamics of plant communities
- Assessing the impact of livestock on the vegetation
- Recording livestock dynamics, mortality and natality rates, sales and slaughter.

In this context several studies were undertaken. Gotzmann (2002) investigated the vegetation dynamics and the impact of grazing on the vegetation cover. Hendricks (1998) studied the livestock dynamics and the impact of livestock on the vegetation. Weidner (1997), Williamson (1998), Wand et al. (1999) and Rundel et al. (1999) investigated the ecology of different plant species of the Richtersveld.

A map of southern African vegetation based on phytosociological data is still non-existent. A basic work in terms of vegetation classification and mapping is given by Acocks (1953/88), known as 'Veld Types of South Africa'. A new collaborative initiative entitled 'the National Vegetation Map of South Africa Project' (VEGMAP) has been installed in order to compile a vegetation map of southern Africa (NBI 2003). It is funded by the Department of Environmental Affairs and Tourism (DEAT) and managed by the National Botanical Institute (NBI), Cape Town. The project emphasizes the need

for detailed documentation of the southern African vegetation as a necessary tool for its careful conservation and management. At any rate the vegetation is directly or indirectly the most important source of food and fuel for the majority of the inhabitants (NBI 2003). The aim of this initiative is to determine the vegetation units of southern Africa as a basis for the map. The database is compiled from Acock's historical data and new data from the contemporary scientific work on vegetation undertaken by universities and state departments.

Detailed vegetation maps in the vicinity of the study area have been rare up until now. A vegetation map of the whole Richtersveld is in preparation by Jürgens. The National Botanical Research Institute in Windhoek, Namibia, is working on a vegetation map of Namibia (Strohbach & Sheuyange 2000). The work on the vegetation map of southern Namaqualand has also been started based on the phytosociological studies of Le Roux (1984). Schmiedel (2002) presented a detailed vegetation map of the Knersvlakte. For the Karoo Region the phytosociological studies of Werger (1978) and Werger & Coetzee (1978) exist.

### **1.1. Aim of the study**

The present study aims to:

- Set up a phytosociological classification;
- Determine the environmental factors which control the vegetation patterns;
- Present a detailed but preliminary vegetation map of the northern Richtersveld.

The vegetation was studied along a coast-inland transect stretching from fixed sand dunes on the coast, along the steep mountain slopes and inner-mountain basins to the hot Orange River valley of the hinterland.

### **1.2. Physical environment**

#### **1.2.1. Geography and definition of landscape units**

The Richtersveld is situated in the north-western corner of the Division of Namaqualand in the Cape Province of South Africa. Forming the natural border between South Africa and Namibia the perennial Orange River skirts the Richtersveld from its mouth upstream with a big bend to the north and north-east. The longitude 17°30' marks the limit to the east (road N 7, Vioolsdrif – Steinkopf), whereas the 29th parallel delimits the southern part (road 382, Port Nolloth – Steinkopf). The Atlantic Ocean gives the natural border to the west (Fig. 1.1).



Fig. 1.1: Topographical map of the Richtersveld. The frame marks the study area, which follows a climatic gradient from coast to inland (after Williamson 2000, modified).

The northerly part of Namaqualand, the Richtersveld, covers approx. 8000 km<sup>2</sup>. It reaches from the Atlantic to about 90 km inland. The maximum north-south extension is 120 km. The coastal plain stretches from the coast to the foothills of the escarpment in a distance of about 40 km. The steep escarpment reaches the Central-African Plateau up

to an elevation of more than 1000 m forming a climatic border. The Vandersterrberg and the Stinkfonteinberge form the north-south aligned mountain range. The Goariep mountains lies off the Vandersterrberg facing to the west. The Rosintjebos mountains join the leeward side of the Vandersterrberg. The highest mountain of the Richtersveld, the Cornellsberg with 1374 m elevation, is part of the Stinkfonteinberge.

The Orange River has carved out a deep gap into the main mountain range especially in the north-south aligned escarpment range, forming deep gorges.

The following classification and definition should provide an orientation to the extensive landscape under focus. Besides other habitat conditions the relief has mainly established the basis for the classification. The names are given according to geomorphologic definitions. Regional names were found in topographical maps but also in 'Tracks and Trails of the Richtersveld' (Reck 1996). Several names of regions, mountains or rivers were provided by indigenous people but most of them derived from European colonists, missionaries and prospectors. The location of landscape units is shown in Fig. 1.2.

**Namaqualand** This is the northern part of the northern Cape Province in South Africa. The borders of which are: Namaland bordering to the north (Namibia), the Bushmanland section of the Karoo (northern Cape Province) to the east, and the west coast of the western Cape Province adjoining to the south.

**Richtersveld** It is the northern part of the Namaqualand. It is subdivided into a coastal plain and a mountainous area.

**Coastal plain** This plain is the northern extension of the Namaqualand Sandveld along the coast of the Atlantic Ocean (Photo A. P2). The relief of the coastal plain slowly ascends along a distance of about 40 km from the Atlantic up to the footslope of the escarpment to an elevation of about 300 to 450 m.

**Coastline** The plain directly bordering the Atlantic Ocean and up to ten kilometres further inland consists of white sand. Further inland from the coast longitudinal sand dunes have formed.

**Inner-coastal plain** It is situated ten kilometres further inland from the coast up to the firm sand ridge, where the white sand is successively followed by red sand. The plain is gently undulating with mainly fixed longitudinal sand dunes.

**Firm sand ridge** Old reddish firm sand forms a long ridge which is increasingly covered by the younger wind-blown red sand nearer to the coast, which together form a patchy pattern. The ridge curves to about 450 m elevation where the rock outcrops Springklipberg and Torkop are located. As the Goariepvlakte and the inner-mountain basins of the escarpment, the firm sand ridge is characterised by *heuweltjies* or Mima-like mounds. These are circular calcrete mounds with a different vegetation cover to that of the surrounding matrix vegetation (see chapter 3.1.2), which give a pock-marked appearance on aerial photographs (Villiers & Söhne 1959).

**Red dune** The topographical shape of the red dune forms an almost longitudinal aligned interrogation mark with a length of 55 km and a height of 70 m from the basis to its top. The loose sand settled behind the leeward site of the firm sand ridge a long time ago. To the east it borders on the Goariepvlaakte.

**Mountain area** The escarpment rises abruptly from the coastal plain to 1000 m elevation as part of the Richtersveld mountains extending to the east. The mountains have a sharp and rocky character with shallow soil pockets. The mountain area is divided into the escarpment range, its plains and basins, and the Goariep region.

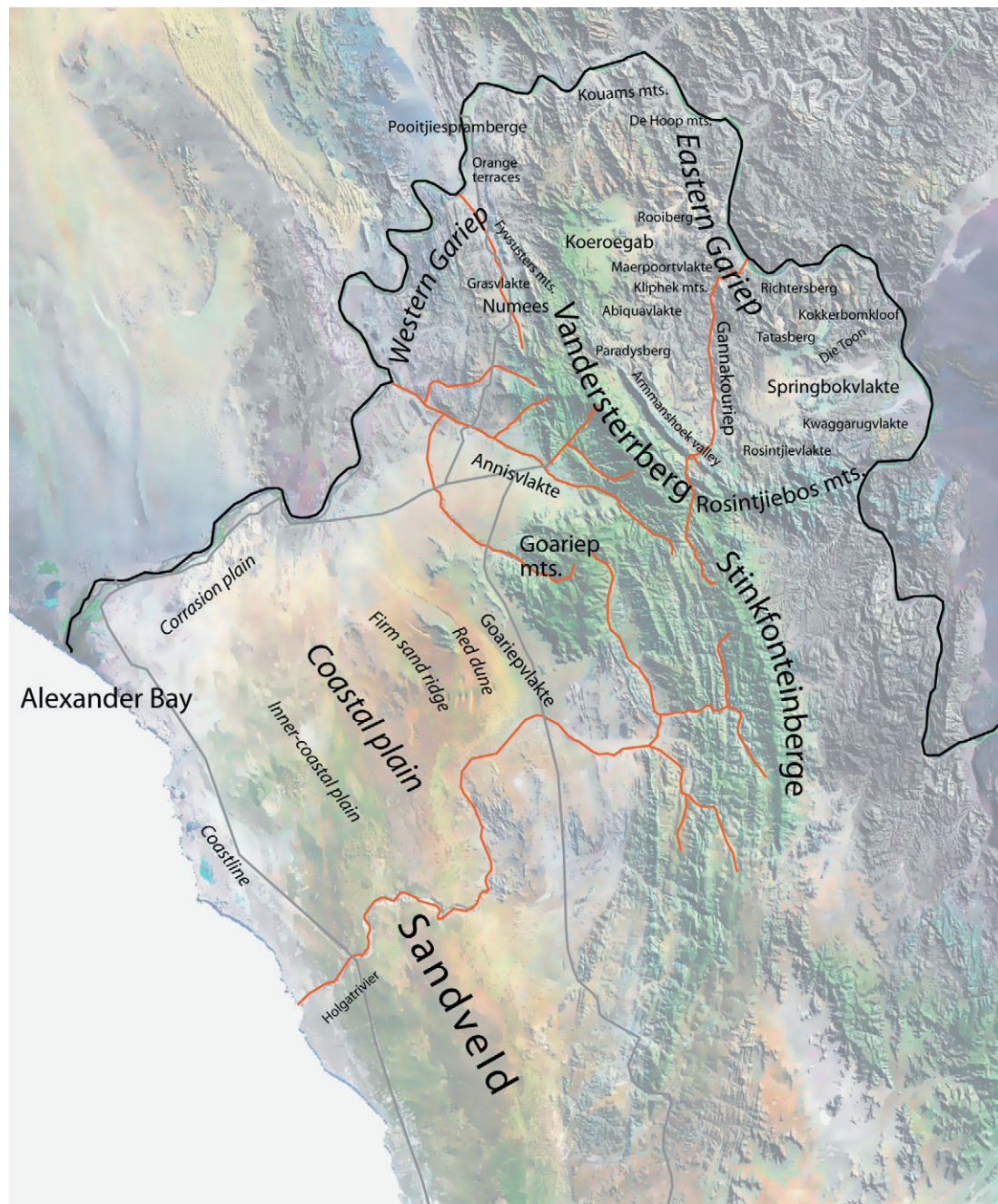


Fig. 1.2: Topographical map of the Richtersveld with features of the defined landscape units.

**Escarpment range** The seasonal soft winter rain has given the escarpment range more rounded valley cross-sections and surfaces. Due to lower evaporation during winter and the softness of the rain, which drains the surface, chemical weathering is possible. The bedrock is frequently covered with a fine-grained soil surface.

**Vandersterrberg - Stinkfonteinberge** These form the escarpment range, which have a north-south alignment.

**Goariep mountains (Ploegberg)** The annex on the west side of the Vandersterrberg - Stinkfonteinberge are the Goariep mountains. The annex to the east is the **Rosintjebos mountains** that form a west-easterly mountain range on the same latitude of the Orange River (Oranje) mouth. The Goariep mountains are special due to its large round granite boulders and rock faces.

**Koeroegab mountains** A half-circle of high eastward facing mountains adjoins the northern part of the escarpment ranges, where the relief slowly descends to the deep carved Orange River valley. The mountain circle is formed by up to 950 m high mountains such as the Peilkop, Kudas Peak and Domorogh mountains surrounding the Koeroegabvlakte.

**Numees mountains** The northerly extension of the Vandersterrberg - Stinkfonteinberge are the Numees and Paradys mountain complex, together with the Helskloof they are known as a region of exceptionally high diversity. The Helskloof is a deep carved ravine aligned to the west and leading into the Numees valley. The eastern descent of the Numees mountains ends in a softly undulating hilly country at Die Koei, which is extensively grazed.

**Plains and basins** Vlaktes are mainly plains with a constant downwards slope of 2° - 5° inclination. They are located on both sides of the Vandersterrberg - Stinkfonteinberge. On the west side they are adjoined to the footslopes of the escarpment and border the coastal plain (Goariepvlakte) and further north the Orange terraces (Annisvlakte, Grasvlakte), whereas, the vlakte on the east side are mainly inner-mountain basins (e.g. Koeroegabvlakte) with a drainage system directing the scarce rainwater to the centre of the concave plains and from there to the end of the basin.

**Silty plains / Goariepvlakte** The Goariepvlakte is situated at the end of the Goariep foothills bordering the coastal plain and thus the red dune. It shows the typical *heuweltjies* or Mima-like mounds.

**Numees valley** This valley is surrounded by the Numees mountains (Photo A. P6). It drains to the west into the enlarged plain Annisvlakte. Here the highest plant diversity within the park was recorded.

**Koeroegabvlakte** As already mentioned this vlakte is situated in the Koeroegab mountains, draining to the east via the Kookrivier (Photo A. P9). This plain lies at a high level as does the Springbokvlakte, about 400 to 600 m. Its surface is also strewn with *heuweltjies*. The Rooiberg is located in front of this drainage system.

**Abiquavlake** This vlakte lies directly adjacent to the Koeroegabvlakte and also drains to the east, but its ground level is about 100 m lower than the former (300- 450 m). This plain is similar to the one previously mentioned, also the *heuweltjies* reach the same density.

**Armmanshoek valley** This valley is situated in the lee of the Vandersterrberg - Stinkfonteinberge and in front of the Numees mountain and the Tswaies mountain ridge, draining to the east.

**Rosintjievlake** This plain is situated in the corner of the Rosintjieberg and the Vandersterrberg - Stinkfonteinberge (Tswaies) exposed to the north-east. Its appearance is very similar to the Koeroegabvlakte.

**Kwaggarugvlakte** This vlakte is the most eastward lying silty plain. Its ground level is 500 - 700 m and is well surrounded by over 900 m high mountain ranges such as the Mount Terror of the Rosintjebos group and the Kwaggarug mountain.

**Gravelly flood plains / Grasvlakte** The vlakte is situated in front of the escarpment, Numees mountains and the Fyvesusters mountains and drains to the north-west. It has a very dry situation due to its low level of 200 - 300 m as part of the arid lower Orange River valley.

**Annisvlakte** The extended Annisvlakte fills the triangle between the high Vandersterrberg and the Goariep mountains. It reaches the same ground level as the latter and faces to the west. It is also part of the lower Orange River valley and therefore exhibits a dry character. Furthermore, signs of over grazing mark this vlakte. The largest local herder town, Khubus, is situated below the footslope of the Vandersterrberg on the Annisvlakte.

**Maerpoortvlakte** Within the park, the Maerpoortvlakte shows the typical appearance of a gravelly flood plain despite being situated directly next to the Koeroegabvlakte. It is situated east of the Koeroegab mountain cycle close to the Rooiberg, and is exposed to the south-east. Its ground level reaches from 300 to 500 m.

**Springbokvlakte** The most eastward and largest plain within the park is situated between the Rosintjebos mountains and the Tatasberg. The Springbokvlakte is gently and almost perfectly symmetrically concave. From about 500 m it has a nearly constant slope down from the west to the Orange River (about 100 m).

**Kokkerbomkloof** Located in between the Tatasberg Complex, the Kokkerbomkloof is the highest vlakte of the park (450 - 650 m). The vlakte slopes down from the Tatasberg south-eastwards in the direction of the Orange River.

**Gariiep region** Gariiep is the indigenous name for the Orange River. The term Gariiep region determines the area surrounding the Orange River valley. The Gariiep is subdivided into a western and an eastern part due to different climatic conditions and floristic compositions.

**Western Gariep** The western Gariep, unlike the eastern Gariep, is climatically influenced by the Atlantic Ocean in terms of fog precipitation. Nevertheless it belongs to the arid part of the Richtersveld owing to the fact that winter rain is scarce and the elevation is low. The mountains of the escarpment extension and the terraces of the Orange River are part of this region. Near the mouth of the Orange River the western Gariep is characterised by high corrosion processes.

**Western Gariep mountains** The Pooitjiespramberge are situated in the north-western loop of the Orange River (Photo A. P12).

**Orange River terraces** The old river terraces craved by drainage lines are ordered along the slow flowing lower Orange River as soon as the valley opens to the south-west.

**Corrasion plain** The area reaching from Beauvallon and Alexander Bay several kilometres to the south, is a special part of the coastal plain. In this zone of strong corrasion processes most of the sand has been blown away or a microhabitat of flat and narrow longitudinal dune bodies has developed (0.5 x 2 m) alternating with nearly bare stone or crust surfaces. The diversity hot spot 'Eastern Gariep Centre' is located here (Jürgens 1997, 1998).

**Eastern Gariep** The eastern part of the Gariep is the driest region of the Richtersveld. In contrast to the western mountain ranges, thunderstorms with high intensity rain leads to a more superficial draining. This causes canyon-like valleys and craggy mountain slopes with a low amount of fine material or soil on the surface.

**Eastern Gariep mountains** The mountains of the eastern Gariep are not as high as the escarpment ranges with elevations of 300 - 400 m. The mountains of De Hoop, Kliphek and Kouams all belong to this hilly landscape. The mountains Richtersberg and Rooiberg are approx. 700 and 900 m.

**Tatasberg** The Tatasberg, also situated within the eastern Gariep mountains, rises to the east of the Richtersveld. Due to its elevation of more than 1000 m and a special geological formation it is described separately. The Tatasberg and Die Toon are the characteristic mountains. Such as the Goariiep mountains to the west, the granite of the Tatasberg Complex weathers into large rounded boulders and rock faces that give a wondrous fairytale landscape with curiously shaped rocks. The Kokkerbomkloof is adjacent to the Tatasberg to the east.

**Gannakouriep region** The Gannakouriep valley is special due to its low ground level of only 250 to 300 m within the high mountainous Richtersveld to the west and east (e.g. Springbokvlakte: 500 m, Koeroegabvlakte: 550 m) and due to its black rock colour and its intrusive dolerite dykes. The surrounding mountains reach 300 to 500 m. The Gannakouriep follows a tectonic line and is connected to the middle part of the even low Abiqua valley.



### 1.2.2. Geology

The open mountain-desert landscape of the Richtersveld is the result of a long sequence of geological events that began 2000 million years ago. Villiers & Söhnge (1959) undertook an extensive study of the geology of the Richtersveld. In their work a detailed description of the geological formations and a map are given. Williamson (1995, 2000) gives a vivid summary of the Richtersveld geological formations and a short description of where they are exposed at the surface. This information is based on the work of Visser

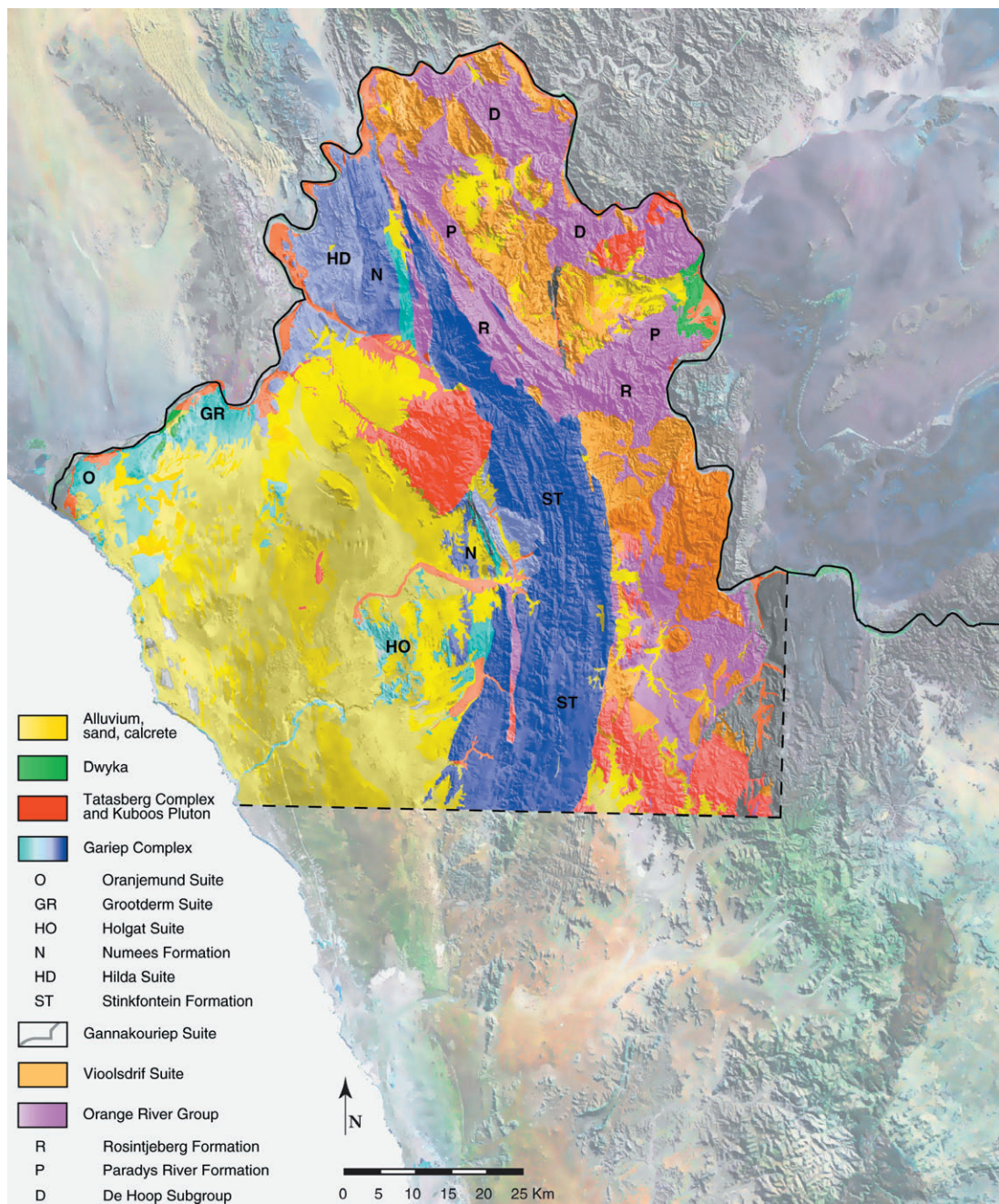


Fig. 1.3: Geological map of the northern Richtersveld (data from Villiers & Söhnge 1959, simplified after Williamson 2000).

et al. (1989), who established a geological classification for southern Africa. A brief introduction of the main formations and their location follows in this section.

When looking at the coast-inland transect of the study area the oldest rocks lie in the eastern Gariep region (Fig. 1.3 and Tab. 1.1). The age of the geological sequences decreases from east to west. The youngest rocks and sediments are to be found along the coastal plain.

#### Orange River Group, ± 2000 m.y.

As already mentioned we have to look to the north-eastern part of the Richtersveld for the oldest rocks, where the eastern Gariep mountains are restricted by the Orange River, its loops turning from west to north. Here the Paradys mountains, the Rosintjebos mountains and the De Hoop mountains are included. The pink coloured rocks of lava, porphyry and tuff are the remains of an ancient belt of island volcanoes.

#### Vioolsdrif Suite, 1900 - 1700 m.y.

The younger Namaqualand basement granites of the Vioolsdrif Suite intrude into the rocks of the Orange River Group. In two north-west-south-easterly aligned bands the orange-brown granite-gneiss nestles among the older rocks: One band spans from the escarpment leeward descent to the central Richtersveld mountain section with the Pooitjiespramberge, Koeroegab mountains, Rooiberg, Maerpoort and Gannakouriep mountains. Southwards, behind the rocks of the Rosintjieberg Formation of the Orange River Group the rocks of the Vioolsdrif Suite continue. The other band is adjacent to the De Hoop Subgroup of the Orange River Group to the east, filling the north-easterly loop of the Orange River.

#### Gannakouriep Suite, 870 - 540 m.y.

During a long geological period the crust of the earth was uplifted and fractured. This dynamic period and fracturing led to the intrusion of magma welling up through the rocks of the Vioolsdrif Suite. Crystalline, dolerite dykes up to one kilometre wide were formed. These black dykes stretch almost south-north along the Gannakouriep valley and between the Sendelingsdrif and the Koeroegabvlakte.

#### Gariep Complex, 660 - 500 m.y.

The Stinkfontein Formation, comprising the oldest rocks of the Gariep Complex dated at 660 million years old, lies between the older rocks of the Orange River Group and the Vioolsdrif Suite on the eastern side and the younger Gariep rocks to the west. It is suggested that the sediments derived from the mountains of the Rosintjieberg Formation to the east and were deposited on the westerly footslopes of these ancient mountains under wet climatic conditions during a cold glacial period. Evidence for this hypothesis are the presence of sedimentary breccias, which represent consolidated scree and talus

Tab. 1.1: Time scale of the geological events in the Richtersveld. (after Williamson 2000, modified).

EONS	ERAS	PERIODS	EPOCHS	AGE MILL. YEARS	RICHTERSVELD GEOLOGICAL EVENTS	LOCATION			
Phanerozoic	Cenozoic	Quaternary	Holocene	0,05	Winter rainfall established Desert spreads	Orange river terraces			
			Pleistocene	2.5					
		Tertiary	Pliocene	4					
			Miocene	7					
			Oligocene	26					
			Eocene	38					
			Palaeocene	54					
	Mesozoic	Cretaceous	(Global extinction)	136	Diamond Pipes	dunes of the Sandveld forming of sand-chocked			
		Jurassic		190	Gondwanaland fragmenting				
		Triassic		245					
	Palaeozoic				(Extensive Ice Age)	Dwyka	lower Springbokvlakte		
								Permian	280
								Carboniferous	345
								Devonian	395
Siurian								430	
Ordovician								500	
Cambrian								570	
Cryptozoic	Proterozoic	Precambrian			Tatsberg and Kuboos Plutons Gannakouriep Suite - 540 ma Nama Group	Tatasberg, Goariep mountains Gannakouriep south-eastern Richtersveld			
							662	Gariep Complex	Escarpment and mountains of the Sandveld Gannakouriep Rooiberg in south-eastern Richtersveld southern Richtersveld west-part of the Eastern Gariep east-part of the Eastern Gariep Paradys River, Rosyntjieberg De Hoop, Rooiberg
							870	Gannakouriep Suite - 870 ma	
							920	Richtersveld Suite	
							1166	South-east granites, gneiss and mica schists	
							1731	Vioolsdrif Suite	
	1990						Vioolsdrif Suite		
	1996						Orange River Group		
	2600								
	Archaeal								3400

derived from the ancient rocks of the Rosintjieberg Formation. The absence of limestone indicates that the sediments were deposited comparatively near to their source under fluvial conditions (Villiers & Söhng 1959). These sediments of resistant quartzite, pink feldspar-rich sandstones and prominent conglomerates, terminated in the unfolding and birth of the modern Vandersterrberg - Stinkfonteinberge (Williamson 2000).

The adjacent sandstones, conglomerates, shales and dolomitic sandstones of the Hilda Suite were deposited on the edge of a shallow ocean 580 million years ago under glacial conditions. The sediments of the Hilda Suite are situated along the eastern Orange River, the eastern Gariep, south of Sendelingsdrif, extending to the Grasvlakte and Helskloof. Some occurrences can be found near Khubus. The tillites of the Numees Formation were almost simultaneously deposited both north and west of the Vandersterrberg, under similar conditions. The sediments of the Holgat Suite, consisting of a large assemblage of rock types with typical tillites towards the top of the sequence, are the result of a slower deposition. The sediments of the Holgat Suite extend from the rocks of the Hilda Suite to the present coastline. To the north-west the Gariep Complex continued with the development of the Grootderm Suite rocks 500 million years ago. These rocks of flat to low hills originate almost entirely from volcanoes. Schist, greywacke and quartzite overlie the volcanic rocks. The cycle of the Gariep Complex is completed by the Oranjemund

Suite that is situated in the north-west corner of the Richtersveld, at Oranjemund. Today the present coastal sand plains overlie the rocks of the Gariep Complex.

Tatasberg Complex and Kuboos Pluton, 530 - 500 m.y.

The Tatasberg and Goariiep mountains complexes were simultaneously formed by the igneous intrusion of magma. The Kuboos Pluton of the modern Goariiep mountains intruded into the Gariep Complex on the west side of the Vandersterrberg - Stinkfonteinberge, whereas the Tatasberg Complex intruded into the oldest rocks of the Orange River Group and the Vioolsdrif Suite in the eastern Gariep region.

Dwyka, ± 300 m.y.

During the Great Ice Age large glaciers moved over the Nabas basin situated at the lower Springbokvlakte. The mud and turbid layers deposited were formed by the ice sheets and abraded the underlying rocks. After the ice had melted, further metamorphism developed orange, pink, brown and black pavements of tillites.

Alluvium, sand, calcrete, 50 m.y.

The drainage system with drainage lines and wide valleys was already established during the Cretaceous period. After the late Cretaceous the climate changed to more arid conditions. At the beginning of the Tertiary period the tributaries of the Orange River dried up completely and the deeply incised valleys became choked with rock-waste and sand, partly wind-borne but largely brought in by surface water (Villiers & Söhnge 1959). The surface of all these sand-choked valleys such as the Springbokvlakte, the Maerpoortvlakte and the Annisvlakte is composed of granite grit with remarkably little fine material. It is suggested that the finer material was partly removed by wind action and deposited in adjacent areas. Much of the sand is now collected in dunes on the coastal plain, for example. Due to higher rainfall in the vicinity of the high mountain ranges (Vandersterrberg - Stinkfonteinberge), the footslopes, such as of the Goariiepvakle and inner-mountain basins e.g. the Koeroegabvlakte and the Abiquavvlakte, received sufficient water to maintain a vegetation capable of preventing the stripping of the surface soil and accumulating large quantities of rock-waste as well as finer material (Villiers & Söhnge 1959).

Today strong thunderstorms are observed in the eastern triangle of the Rosintjebos mountains and Vandersterrberg - Stinkfonteinberge, coming from the east during the summer. Similar observations are made for the vicinity around Sendelingsdrif. During these thunderstorms a large quantity of water falls in a short time and the surface of the sandy plains, such as the Springbokvlakte, begins to move, so that extended mud masses from the whole plain slip down to the lower Orange valley. This type of plain is therefore called a sheet wash plain. This could also be one reason for the flatness and coarseness of the sandy plains as the fine material is additionally removed by water

action. The cyclonal rain in winter falls softly and over a long period so that the raindrops penetrate the dry surface of the plains obviously in the western part of the Richtersveld. Erosion is dominant in the eastern part, due to low surface drainage.

At the same time as the valleys and plains were choked with rock-waste, the clayey sandy soil of the coastal belt was developed under hot conditions. These have been exposed where the wind-blown sand has been removed by wind action. This reddish firm sand is characterised by a prolific development of more or less circular pimple mounds of calcrete (Mima-like mounds, see chapter 3.1.2.1), which can also be observed on the silty sands of the inner-mountain basins of the mountain region. It is inferred that the sand was formed mainly by the decomposition of the underlying formations, owing to the fact that no fossils were found in the firm sand of the coastal plain. This process could have taken place under weathering conditions between dunes whilst the latter were still shifting and also after they had become more or less fixed (Villiers and Söhnge 1959). The wind-blown sand, which forms these dunes, has its origins possibly from the extended surfaces of the arid sandy plains within the mountain region, as previously mentioned.

During the Pleistocene period, the retreat of the sea caused a further lowering of the coastal area so that parts of the continental shelf were uncovered. River terraces were left exposed and due to further lateral erosion, these diamondiferous terraces were laid bare. These terraces lie along the lower Orange River valley in the western Gariep (Williamson 2000) and are today the focus of the mining companies.

### **1.2.3. Soils**

The soils of arid regions are mostly weakly developed. After the low water resource, which reduces the chemical weathering, the wind in combination with low vegetation cover is the main impediment to pedogenic processes. Low precipitation with simultaneously high transpiration leads to reduced washout and little movement of clay. On the other hand readily soluble salts are enriched at the surface by ascendant soil water that causes basic pH-values. The humus portion is low (under 1 %).

The infiltration of water is impeded, because the air of the soil pores could only slowly leak out of the dried soils. The highest infiltration rate is reached by substrates of homogeneous grain size and a low portion of fine material (Besler 1992). This is true for e.g. sands. Typical for the soils of the study area is the development of crusts by local solution and concretion processes. At the coastline gypsum crusts predominate, whereas inland the occurrence of lime crusts increases (Besler 1992). While it is suggested that lime crusts are a product of a fossil development during a pedogenic period (Besler 1992), the gypsum crusts could also have developed under recent climatic conditions (Watson 1988). The soil surface is often protected against erosion by a 1 mm thin physical and microbial crust.

Although a detailed soil classification and map of the Richtersveld was not available, several studies have focused on the soil properties of the Richtersveld and their ecological value for the vegetation. Jähnig (1993) investigated several selected soil catena, whereas Boenigk (1998) and Osterloh (2000) studied the soils of the stock posts. Oguz (1999) and Stöcker (1999) worked on the vegetation and soil properties of the Sandveld.

According to the FAO (1989) the soils of the Richtersveld belong to the main soil groups of arenosols, on the coastal sand plain (Sandveld), and leptosols within the mountain region. Arenosols are characterised by their low pool of weatherable minerals and their low silt/clay to sand ratio. The parent material is aeolian sand or sands derived from aeolian deposits. Leptosols are shallow soils with weak profile differentiation.

South Africa has its own soil system according to the classification of Van der Merwe (1962), which is based on climatic features. In the reclassification of Loxton (1962) and in the map of Harmes (1978), based on the classification of Van der Merwe, the soils are subdivided by their morphological and genetic characteristics. A more detailed map for the soils of the Karoo, presented by Ellis (1986), orders the soils to the main landscape units. This focus pays less attention to the soil characteristics but stresses the categorisation of landscape units. By collecting the most important soil characteristics for every landscape unit, the soil characteristics are strongly standardised or left unnamed.

#### **1.2.4. Climate**

The climate of the western coast of southern Africa forms a complex situation that has similarities with other regions of the world. The aridity of the Namib Desert is caused by its close vicinity to a cold sea current parallel to the coast - the Benguela current, this effect can also be found in the Sechura Desert (Peru) and in the Atacama (Chile). The cold surface of the sea leads to a descent of the air masses which in turn builds up an inversion layer. This inversion layer, which is further stabilized by the south-eastern trade winds, prevents the ascent of air masses and therefore condensation and resulting precipitation.

According to the climatic data available and model outputs (Schulze et al. 1996) the climate of the Richtersveld and adjoining areas clearly shows a transient character (Fig. 1.4). Two major climate regions border along the north-south aligned mountain ridge of the escarpment: The warm temperate winter rainfall on the west side and the non-seasonal rainfall on the east side (Fig. 1.5). The regular summer rainfall regime is adjoined further east and to the north.

The west wind drift reaches the southern Namib only in winter when the ITCZ (Inner Tropical Convergence Zone) migrates further north. Precipitation within this zone occurs during the coldest months of May to September, varying from c. 50 mm p.a. at the coast, c. 100 mm in the valleys and lowlands, to >150 mm on the Richtersveld mountain

tops. The precipitation rate in the non-seasonal rainfall zone is low, unpredictable, and rain often falls in intensive thunderstorms, as is normally observed under summer rain conditions.

The descending air over the cold sea surface condenses and develops fog banks. The Atlantic-Benguela anticyclone causes strong sea mists to flow eastwards over the coastal plain and into the low-lying Orange River valley, especially in winter when the zenith position of the sun is well to the north. The reduced radiation load results in rather cold temperate conditions. In contrast, the temperature in the mountains of the escarpment varies considerably from winter to summer, and the diurnal amplitude is high. There is an increased probability of frost at higher altitudes and further east into the interior, and the cold winter temperatures are frequently interrupted by hot easterly

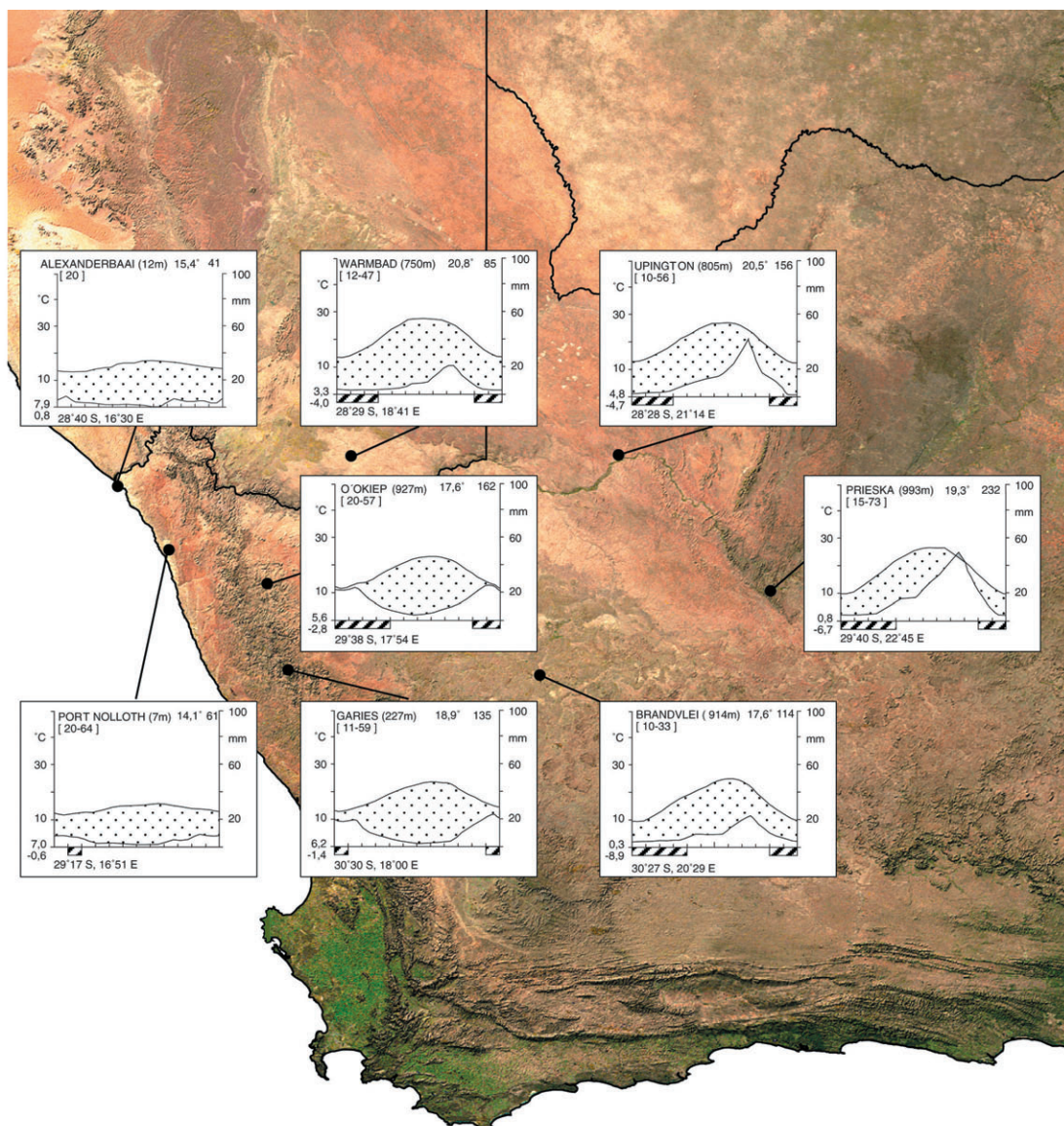


Fig. 1.4: Climatic diagrams of eight meteorological stations located within the north-western Cape Region (Walter & Lieth 1965).

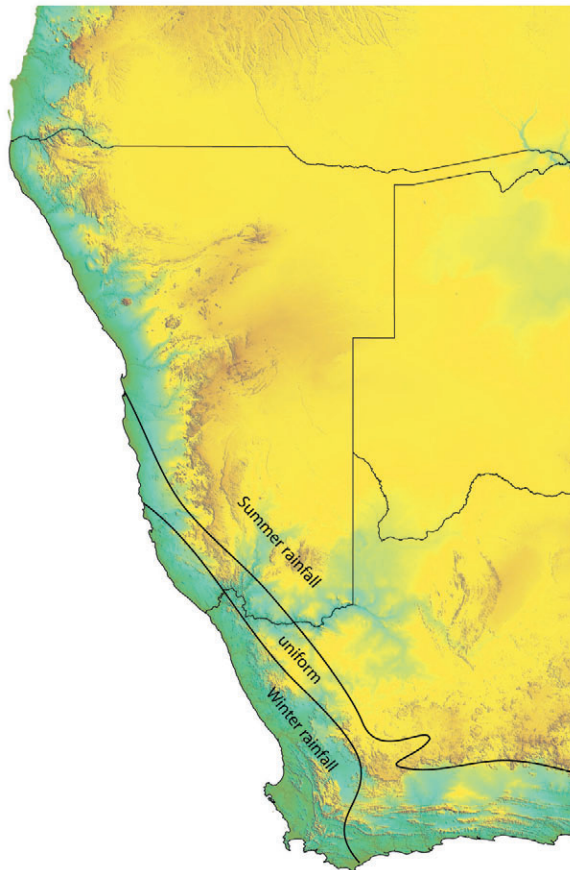


Fig. 1.5: The two major climate regimes, winter rainfall and summer rainfall on the western coast of southern Africa. The winter rainfall regime borders a zone of low, non-seasonal precipitation that is followed farther inland to the east and north by the summer rainfall regime proper.

„berg winds“. Cold air masses, on the plains of the old land surface further inland, slowly flow westwards following the relief descent from the east (Drakensberge) to the west of the African plate and fall down abruptly along the escarpment descent. Stormy hot winds reach the footslopes of the escarpment and the coastal plain along with the adiabatic increasing temperature.

### 1.3. Biotic settings

#### 1.3.1. Flora and vegetation

##### *Flora*

The flora of southern Africa is, with about 21000 indigenous species (Arnold & De Wet 1993), among the richest in the world for similar sized areas (Goldblatt 1978; Gibbs Russell 1985; Cowling et al. 1989; Cowling & Hilton-Taylor 1994, Cowling & Hilton-Taylor 1997). The Succulent Karoo records more than 5000 species per 100251 km<sup>2</sup>, which is the highest species richness for semi-arid vegetation, out of which 50 % are endemic (Cowling et al. 1989, Milton et al. 1997).

The flora of the Richtersveld contains about 1615 species up to now, from which 140 species are endemic (Williamson 2000). The majority of the endemic species occur on



the higher altitudes of the escarpment as well as along the Orange River valley (Gariep). Some of the species, mainly belonging to the most common family of the Richtersveld, the Mesembryanthemaceae (50 genera with 255 species), have not been described up until now. The families Asteraceae and Crassulaceae are highly represented with 200 species of 27 genera and 88 species of four genera (Williamson 2000). The floristic recording of the Richtersveld flora is mainly attributed to van Jaarsveld (1980, 1981, 1989, 1992, 1994), Williamson (1990, 1992, 1994, 1995, 1998, 2000), Leach (1984), Manning (1990), Midgley (1997), Pierce (1997) Gerbaulet & Schollenberger (1993).

### *Phytogeography*

A detailed review of early research on phytogeography of southern Africa is compiled by Cowling & Hilton-Taylor (1997 with comprehensive literature). Based mainly on their work some remarkable points of the development are given in this section.

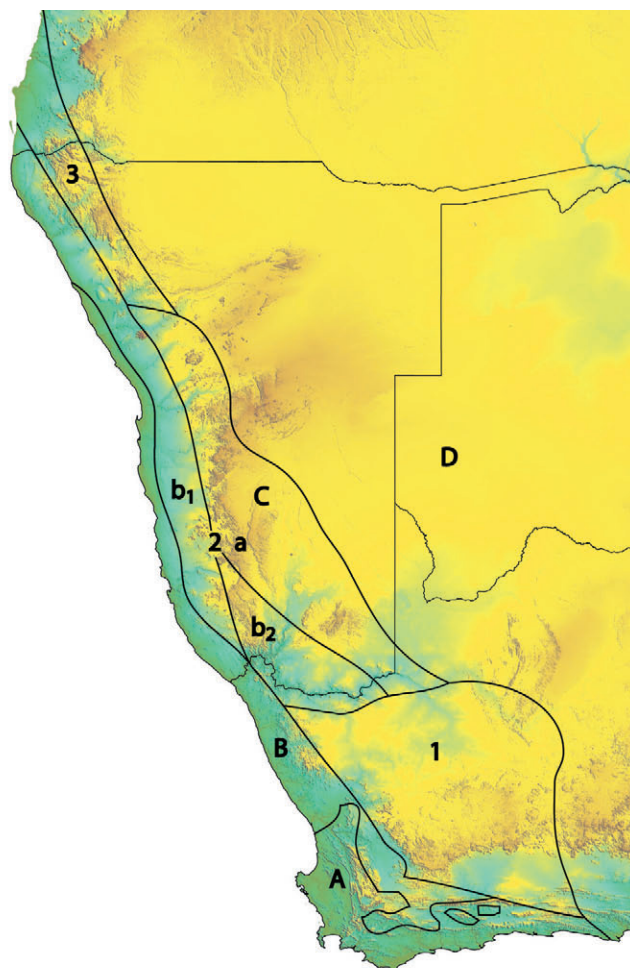
Bolus (1875, 1886, 1905), Rehman (1880), Engler (1882) and Marloth (1887) recognized a south-western region (Cape Region), a Karoo region, a Kalahari region and eastern seaboard region in their early attempts to divide the sub-continental flora. These examinations led to the subdivision in a *Cape Floristic Kingdom* for the Cape region and a distinct *Palaeotropis Kingdom*, which covers the rest of the subcontinent (Takhtajan 1969). A finer subdivision of the area resulted from examinations by Marloth (1908), Pole Evans (1922) and Acocks (1953). Lebrun (1947), Monod (1957), White (1965, 1971), Troupin (1966) and Good (1974) defined the subcontinent's phytogeography in an Africa-wide context. Werger (1978a) combined the work of his predecessors into a synthetic phytogeographic map for southern and South-Central Africa. The phytogeographic systems of Werger (1978a, 1986) and White (1971, 1976, 1983) are the most introduced and widely accepted (Jürgens 1991, Cowling & Hilton-Taylor 1997). White (1976) subdivided the flora of southern Africa into six different units: Cape Region, Afromontane Region, Tongaland-Pondoland Region, Karoo-Namib Region, Kalahari-Highveld Transition Zone and Zambezian Region. Werger (1978a) also defined a Karoo-Namib Region, which falls entirely into the *Palaeotropis*. Furthermore his subdivision differs in some respects from the phytochorological subdivision of White (1976). Werger ordered the flora into seven different units: Guineo-Congolian Region, Indian Ocean Coastal Belt, Sudano-Zambezian Region, Afromontane Region, Afro-alpine Region, Karoo-Namib Region and *Capensis*.

Jürgens (1991) proposed a split of the Karoo-Namib Region *sensu* Werger (1978a) and White (1976, 1983) into two major units, the Succulent Karoo Region and the Nama Karoo Region (Fig. 1.6). The separation into two different floristic regions was necessary because the Karoo-Namib Region was counted to belong to the Sudano-Zambezian Region of the *Palaeotropis* (Werger 1978a). Only the Nama Karoo Region is part of the *Palaeotropis*, the taxa of the Succulent Karoo show floristic relationships to the *Greater Cape Flora*. Jürgens (1991) subdivided the *Greater Cape Flora* into the Cape Floristic

Region and the Succulent Karoo Region, whereas the Nama Karoo Region is part of the *Palaeotropis* such as the Sudano-Zambezian Region. The Succulent Karoo Region is further subdivided into the Namaqualand-Namib Domain and the southern Karoo Domain. The Nama Karoo Region is split into the Namaland Domain, the eastern Karoo Domain and the Damaraland-Kaokoland Domain. Within the Richtersveld-Namib area Jürgens (1991) (Fig. 1.7) proposed a further separation of the Namaqualand-Namib Domain into the southern Namib District (Namibian west coast), to which the western Gariep Circle/Centre of the lower Orange River valley is counted, the Namaqualand-Sandveld District (South African west coast) and the Richtersveld Mountain District (mountainous region of the Richtersveld). The adjacent part of the Nama Karoo Region in the east is the eastern Gariep District of the Namaland Domain.

### *Biomes of southern Africa*

Fig. 1.6: *Phytogeographic division of the Karoo-Namib Region after Jürgens (1991). The Greater Cape Floral Kingdom comprises the Cape Floristic Region (A) and afro-montane regions further east, and the Succulent Karoo Region (B). The Palaeotropical Kingdom comprises the Nama Karoo Region (C), the Sudano-Zambezian Region (D), and other phytochoria to the north and east. The Nama Karoo Region is subdivided into: 1 = eastern Karoo Domain; 2 = Namaland Domain (subdivided into a = Namaland Subdomain, b = Namib Subdomain, b<sub>1</sub> = Namib District, b<sub>2</sub> = eastern Gariep District) and 3 = Damaraland-Kaokoland Domain (redrawn from Jürgens 1991).*



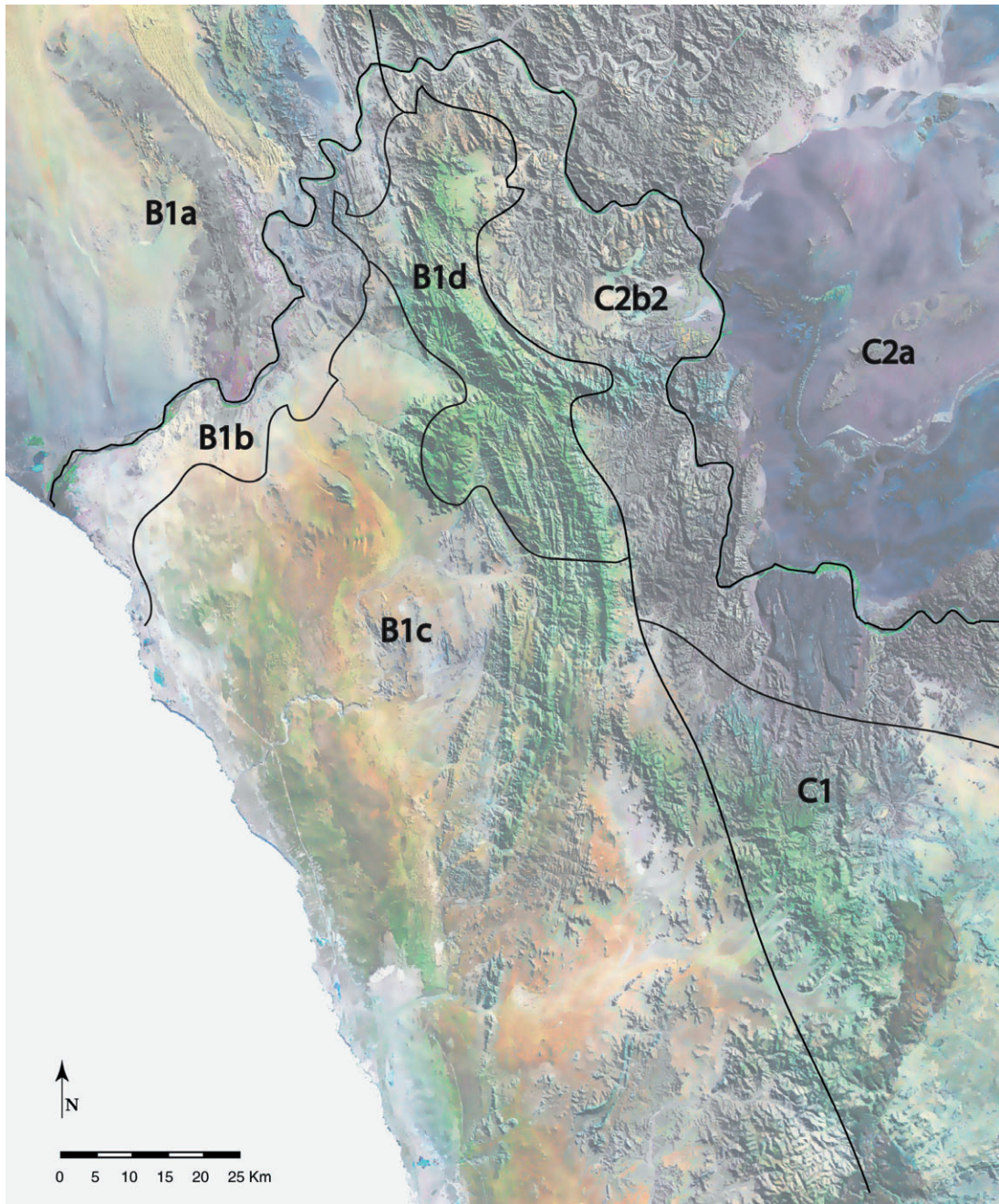


Fig. 1.7: Phytogeographical division of the Richtersveld according to Jürgens (1991). Abbreviations (underlined are the floristic units that are represented in the Richtersveld):

*Greater Cape Flora*

- A — Cape Floristic Region  
 B — Succulent Karoo Region  
   1 — Namaqualand-Namib Domain  
     a — southern Namib District  
     b — western Gariiep Circle  
     c — Namaqualand Sandveld District  
     d — western Richtersveld Mountain District  
   2 — southern Karoo Domain

*Palaeotropis*

- C — Nama Karoo Region  
   1 — eastern Karoo Domain  
   2 — Namaland Domain  
     a — Namaland Subdomain  
     b — Namib Subdomain  
       b1 — Namib District  
       b2 — eastern Gariiep District  
   3 — Damaraland-Kaokoland Domain  
 D — Sudano-Zambeziian Region

Rutherford and Westfall (1986) identified seven biome units for southern Africa based on the dominance of four plant life forms, phanerophytes, chamaephytes, hemicryptophytes and therophytes (Fig. 1.8). The seven biomes are Desert, Grassland, Savanna, Succulent Karoo, Nama Karoo, Fynbos and Forest. Uni-dominance of phanerophytes (P), chamaephytes (Ch), hemicryptophytes (H) and therophytes (T) represent the Forest, Succulent Karoo, Grassland and Desert biomes. Intersection sets determine the Savanna (H, P), Nama Karoo (H, Ch) and Fynbos (H, P, Ch). The Desert biome contains a few areas of co-dominance with chamaephytes or with hemicryptophytes in areas of transition to Succulent Karoo and Nama Karoo (Rutherford 1997). The biome units are not determined on the basis of floristic or phylogenetic composition; therefore a coincidence with phytochoria is not necessary. Independent studies (Gibbs Russell 1987, Cowling et al. 1989, Jürgens 1991) on the species relationships among the main biomes showed a floristic distinction of each biome, except to some extent the Nama Karoo (forest was not analysed) (Rutherford 1997).

*Phytosociological research in the Richtersveld*

Published studies on the phytosociology of the study area and the vicinity have been scarce up until now. Jürgens studied the vegetation of the Richtersveld for about 18 years. More than 1000 relevés form the basis of the vegetation map that is in preparation by Jürgens. The National Botanical Research Institute in Windhoek joined the phytosociological work for a vegetation map of Namibia, which is also in preparation (Strohbach & Sheuyange 2000). The phytosociological studies of Le Roux (1984) form the basis for a vegetation map of southern Namaqualand.

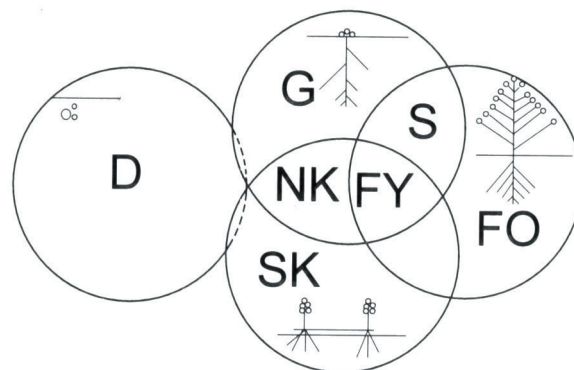


Fig. 1.8: Dominance or co-dominance of four plant life form sets in relation to biomes. Phanerophytes are depicted on the right, chamaephytes below, hemicryptophytes above and therophytes on the left. The biomes are: FO = Forest; G = Grassland; SK = Succulent Karoo; D = desert; NK = Nama Karoo; S = Savanna and FY = Fynbos (redrawn from Rutherford (1997)).

Phytosociological studies for the Karoo Region (Werger 1978b, Werger & Coetsee 1978) also exist.

#### *Vegetation history*

A comprehensive account of the vegetation history of southern Africa is presented by Scott et al. (1997). According to this the vegetation dynamics during the Quaternary period for south-western Africa is briefly summarized here.

During the Quaternary, and probably before, modern biomes were already well established. The evidence for this suggestion is derived from old pollen profiles of the Pretoria Saltpan and Port Durnford. During this period marked cycles of vegetation change occurred which resulted in wide shifts in biome composition and boundaries.

A transition from cooler to warmer climatic conditions in a constant dry environment is assumed for the late Pleistocene to the early Holocene. A shift within the floristic assemblages is shown in the preliminary palynological data from spring deposits at Eksteenfontein, Richtersveld. The assemblages of predominantly Chenopodiaceae / Amaranthaceae type and certain Asteraceae pollen before 10700 BP changes to assemblages totally dominated by pollen of the Aizoaceae / Mesembryanthemaceae type 10700 - 8450 BP (Scott et al. 1995). This climatic change could also have had an effect on the Cape region where pollen data from the Cedarberg show that more succulents occupied the northern Fynbos at c. 8000 BP (Scott 1994). Therefore the Succulent Karoo boundary may have moved southward during that period.

Scott (1987b, 1996), Beaumont et al. (1992) suggest a much wider distribution for the Nama Karoo biome in the interior of southern Africa by the end of Pleistocene (c. 10400 BP) than at present (records from *Equus* and *Wonderwerk*, southern Kalahari). The portion of grasses in the Nama Karoo increased from the early to the middle Holocene (Bousman et al. 1988, Scott 1993) but the grass to shrub ratios continued alternating. Brain & Brain (1977) inferred from micro mammalian evidence (Mirabebe Shelter) that the desert biome was grassier at c. 6500 BP. Scott et al. (1997) conclude that early types of Fynbos, semi-arid, succulent scrublands and desert vegetation of the south-western Cape, the west coast and the Karoo, only became established by the end of the Miocene, i.e. more or less at the same time as modern plant communities on other continents.

#### *Vegetation history of the Holocene*

The establishment of succulent rich dwarf shrub-land or grassland in Namaqualand took place by the late Pleistocene (Scott 1995) as the climate changed from cooler to warmer conditions. The karroid scrubland was forced back to the inland in the east. During the Holocene the Nama Karoo biome resisted in its formation character but the portion of grassy hemicryptophytes and phanerophytes were subject to fluctuations in response to temperature and moisture. During cooler and wetter conditions the portion

of perennial grasses and woody taxa increased, whereas it decreased under warmer and drier conditions.

The archaeo-zoological remains, tentatively identified as blesbok, point to greater grass cover in the eastern Richtersveld at 2000 BP (Webley 1993) compared to the recent vegetation composition with a low portion of grasses. The charcoal remains could probably originate from more substantial woody vegetation than is presently found. The archaeological remains led to the conclusion that there was higher precipitation in the eastern Richtersveld at 2000 BP than today (Webley 1993).

### **1.3.2. Present and former land use - history of the Richtersveld National Park**

#### *Former land use*

Since the early Stone Age the environment of the Karoo has been impacted by human use. While the economies of the inhabitants is not well-known, it has been established that the diet of *Homo erectus* consisted mainly of large mammals such as elephant, rhino, hippo, giant alcelaphine, giant buffalo and smaller animals such as pigs and bushbuck (Klein 1988). It is assumed that humans chased other carnivores away from their kills in order to obtain meat food (Smith 1999).

Unlike *Homo erectus*, *H. sapiens* were capable of hunting animals, which are bigger than themselves on the basis of a newly developed tool technology. The flake tools for example were hafted onto a wooden shaft that could be thrown. The transition of *H. erectus* to *H. sapiens* is presumed to have taken place around 250000 years ago.

The humans of the early and middle Stone Age were obviously hunter and gatherers. Vincent's study (1985) gives indications that exploitation of underground plant foods such as geophytes took place in the Savanna zone of East Africa and maybe also in the Karoo.

The appearance of modern people, *H. sapiens sapiens*, probably occurred during the later Stone Age, around 40000 years ago (Smith 1999). A new phase of development derived from these modern people, including a social organization based on family life, sexual division of labour and equal distribution of product. Reliable resources allowed the hunters to stay in one place for most of the year, which resulted in food storage. Such economic wealth can create surplus and leads to an increasing population density.

Roughly 2000 years ago the first agricultural humans appeared in southern Africa. They brought domestic animals and plants and pottery with them. With their appearance the aboriginal hunter and gatherers fell under existential pressure. The increasing impact on the hunter was slow in the beginning but it gradually pushed them more and more onto marginal grazing lands. This was mostly due to the fact that the pastoralist's

domestic animals competed for the grazing land with the hunter's traditional prey species, which in the end was drastically reduced (Smith 1999).

For the period of ca. 3800 to 3100 BP Webley et al. (1993) found evidence of hunter-gatherer occupation in the Richtersveld, which were derived from an excavation site at Die Toon (north-eastern Richtersveld). The distance of the site to the Orange River is at least 15 km in both the easterly and northerly direction. This is probably the reason for the very rare occurrence of archaeological deposits, indicating only brief visits to the site, possibly only in years of partially good rainfall. Archaeological work in both southern Namibia and Namaqualand suggest an increase in population density after 2000 BP, which may be linked to the arrival of pastoralist groups in this area introducing the domestic sheep (Webley et al. 1993). On the banks of the Orange River at Jakkalsberg (north-west of the Richtersveld) two pastoralist sites were discovered, dated around 1300 BP (Brink & Webley 1996, Miller & Webley 1994, Webley 1997). Faunal remains are predominantly those of young sheep. The site at Bloeddrift (north-west of the Richtersveld) gives evidence of both hunter and pastoralists dated around 355 BP (Smith 2001).

The Orange River and its hinterland were predominantly inhabited by Khoisan societies in the 18th century (Penn 1995). The San people were hunter and gatherers occupying the high lying regions to the east and south-east, whereas the Khoi pastoralists herded their livestock on the Orange River islands. The Khoi societies were split into the Little Namaqua living in the Little Namaqualand, located south of the Orange River, the Great Namaqua of the Great Namaqualand, which was situated north of the Orange River (today known as Namaland), and the Einiqua occupying the east.

The San people were divided into the Sandveld San on the western coast of Namaqualand and the Bushmanland San living in the Bushmanland, Kalahari. The Sandveld San worked as clients for the Namaqua and received protection from this dominating society. However, not all San worked for the Khoi. The more powerful Bushmanland San were enemies of the Namaqua.

During the 18th century the European colonists, coming from the Cape region, pushed slowly but unstoppably forward to the north. Namaqualand served for a long time as a rear guard area against European settlers for Khoekhoe and other displaced groups of the Cape because of its seclusion in the period of colonisation. Few expeditions occurred within this time such as that of Commander Simon van der Stel who led the first Europeans to the Namaqualand in 1685. The Europeans learned from this expedition that the Namaqua were rich in cattle but not numerous. They counted eight to nine kraals (Penn 1995). Encouraged by this experience Europeans began to settle in Namaqualand in 1750 as ivory hunters or livestock traders and raiders. Nineteen white stock-farmers were reported in Namaqualand during this period (Penn 1995).

By 1780 the river had become a zone of terror, as a consequence of the colonial impact shattering the old order, transforming the pre-existing social and economic

networks and introducing an era of violent insecurity. Frontier men of varied origins (Europeans, slaves, „Bastaards“, Khoi, „Bastaard-Hottentots“, San and Oorlams) formed predatory commando gangs which robbed weaker groups of their livestock. The missionaries began their activities during this period of chaos and destruction. The first missionaries arrived in the frontier zone in 1799. In the condition of anarchy, which had accompanied the disintegration of traditional societies along the river, conversion to Christianity offered social, political and economic advantages (Penn 1995).

In 1805 the London Missionary Society started in Namaqualand. More than three decades later (1840) the London Missionary handed over to the ‚Rheinische Missionsgesellschaft‘ (Berzborn 2002). The mission stations gave the local people protection against the Bure and Basters, because the colonial government assured the indigenous people the access to the land around the mission stations (Strassberger 1969 in Berzborn 2002). Through this system, the pastoral-nomadic economy continued to be possible in the Richtersveld. This was not true for the region around the western Cape at the end of the 19th century because white settlers occupied extensive land. The mission station ‚Richtersveld‘, around which the village Khubus had developed, was set up in 1842. In December 1847 Namaqualand was integrated into the Cape colony (Berzborn 2002).

In the 20th century, during the apartheid regime, the Richtersveld was one of five similar administrative areas situated in the north-western Cape which were demarcated as Rural Reserves Act of 1957 (Carstens 1966 in Mussgnug 1995). The other four reserves being Komaggas, Concordia, Leliefontein and Steinkopf. Many people of different ethnic groups were displaced from the Cape region to the Richtersveld. These people live today in the villages Eksteenfontein and Lekkersing (Berzborn 2001). During apartheid the indigenous language *Nama* was forbidden in the schools. Therefore Afrikaans is the language most widely spoken in the Richtersveld today. Since the breakdown of apartheid the political climate has changed. Personal development and a new-formed identity gained more significance. The *Nama* found the way back to their traditional authority structure and their language. The government and the NGO's supported them in their efforts. The support of *Nama* is becoming a symbol of winning back freedom and ethnic identity in the post apartheid period. The language *Nama* has been re-introduced into the school at Khubus since 1999 (Berzborn 2002).

#### *Recent land use*

The traditional life-style of the *Nama* people was based on nomadic pastoralism. This economic system has mainly dwindled in southern Africa, the Richtersveld being one of the last regions to preserve it. It is well adapted to arid regions. The herders and their



flocks move over long distances to overcome the scarce and erratic precipitation, thus avoiding the over grazing that would follow a sedentary life-style (SANP 1997).

Socio-economic and political factors have caused a transition from a fully nomadic way of life to one of semi-nomadism. In the northern Richtersveld most stock farmers have permanent homes in the villages of Khubus or Sanddrif and occupy stock posts while herding their flocks (SANP 1997). These stock posts are distributed throughout the Richtersveld, along the Orange River valley and within the mountain region with its footslopes. As a type of transhumance the movement of the farmers and their flocks follow the seasonal rhythm of precipitation. The smallstock herders make use of the grazing along the Orange River in the dry summer, when goats and sheep may drink twice a day from the river, while moving to the foothills of the mountains in winter after the rainfall. This protects the evergreen Orange River valley against over grazing, while the short spring flowering of ephemeral meadows is optimally exploited. The flock mainly consists of goats; only a small number of sheep or cattle are added. The goats are able to resist drought by obtaining all of the water necessary out of the green, mostly succulent vegetation. Whereas, sheep and cattle have to drink water once or twice a day (Mussgnug 1995).

#### *Richtersveld National Park*

In 1991 an area of 162444 ha in the northern Richtersveld was declared a national park. The management plan for the Richtersveld Park is unique to southern Africa. While in other national parks the indigenous habitants were forced to leave their land, the *Nama* of the Richtersveld are part of the park management. The land belonged to the *Nama* people, and without their consent and cooperation the establishment of a national park was not possible. The Richtersveld communities and the National Parks Board jointly manage the park. „The management plan identifies two major conservation objectives of equal importance: the preservation of the traditional life-style and culture of the *Nama* people together with associated forms of sustainable use of the land and conservation of the great biodiversity and essential ecological processes that characterise the Richtersveld.“ (SANP 1997). Altogether 26 herders and their families have the right to use the land within the park for their traditional semi-nomadism, but the grazing is restricted by certain rules. The number of livestock within the park is limited to 6600 Small Stock Units. One Small Stock Unit is one goat or one sheep and one cattle is the same as five Small Stock Units.

The lack of large wild mammals in the Richtersveld is a result of the activities of European hunters over the last hundred years. Most of the large mammals were totally exterminated. Certainly, the park's attractiveness for the tourists will increase through the re-introduction of wild herds of antelopes or zebras etc.

While the northern part of the Richtersveld is used as communal land, the southern part has been separated into economic units since 1984, as in the whole Namaqualand

and other South African rural reserves. It was assumed that private ownership prevents degradation. Boluis Baster, who was replaced in 1949 and who dominated the political institutions of the southern Richtersveld, approved the establishment of economic units. The indigenous Richtersveld population, who were mostly withdrawn to Koeboes (Khubus) and Sanddrif, were not able to prevent their land being taken into private ownership. In 1989 the economic units were abolished by a court decision (Berzborn 2002).

Along the Orange River a new agricultural development took place. An irrigation plant for mainly citrus fruits and fodder plants was established. Although this part of the Orange River valley resists as natural reserve. Dry-land cultivation is not possible.

In 1926 diamonds were found along the coastal plain. This development has had a significant influence, so that the number of inhabitants largely increased. Today two large mining communities exist, Alexkor and TransHex. The Richtersveld community is also an owner of mining allowances, so that private people, *klynmyners*, also dig for diamonds. Diamond occurrence are concentrated on the sea ground and in the Orange River terraces. The villages Alexander Bay and Sendelingsdrif have been developed from mining communities. In the past other mineral resources, such as copper, were found but these resources did not reach quantities that made exploitation profitable.

After the apartheid regime, the new South African government has been obliged to eliminate the inequality of land use, education, health, water supply etc. caused by racial discriminating laws. With this background the Richtersveld community has been taking action since 1997 to regain their land, which was gradually lost to the state mine Alexkor (Berzborn 2002).

## 2. Methods

### 2.1. Sampling procedure

#### *Fieldwork*

The plot locations were chosen by the common criteria of homogeneity. The minimal area to be sampled in each community was determined several times by starting out with a square meter plot and enlarging it gradually until further enlargement no longer added new species to the species list. This determination was made on species-rich dwarf shrub formation but the resulting size was also used as a standard for other communities in the drier eastern part of the Richtersveld. The determined standard plot size of 10 x 10 m = 100 m<sup>2</sup> was also used for phytosociological investigations within and in the surrounding vicinities of the Richtersveld. This applies to the following regions, studied by N. Jürgen's work group: southern Namaqualand, Knersvlakte, Bushmanland (Pofadder region), Little Karoo and Warmbad region, Sperrgebiet, Namaland, Central Namib in Namibia (e.g. the MSc and PhD theses: Schulte 1994, Schmiedel 2002, Gotzmann 2002, Schüttler 2002, Oguz 1998, Stöcker 1998, Boenigk 1998, Osterloh 2000, Jacobs 1996, Hachfeld 1996 and unpublished data of N. Jürgen). A standardised plot size enables the opportunity to compare the vegetation of different formations such as semi-desert vegetation, dwarf shrub-land and scrubland of more humid parts of the Karoo. This method has also been used in north-east Africa (Bornkamm 1990).

Within the four basic landscape units, coastal plain, escarpment range, Gariep mountains and plains (vlakte), the vegetation was recorded on 871 relevés (Fig. 2.1, A. 12). The relevés were made during winter at the end of the rainy season (July to October) in the years 1996 to 1999 and 2002. For every plot the following site description was recorded:

- Habitat type: sand plain, dune crest, inter-dune, slope, footslope, drainage line, flood plain/sheet wash plain etc.
- GPS reading (Global Position System giving the geographic coordinates)
- Elevation [m]
- Slope inclination [°]
- Slope exposition [°]
- Surface characteristics:
  - cover of bedrock, boulders, pebbles, gravel and fine fraction [%]
- Soil texture employing the standardised finger test outlined in the soil survey standards (*Bodenkartieranleitung*, AG Boden 1994)

For representative sites soil samples were taken and the soil profile was described. The soil analysis is described in section 2.3.

The following characteristics of the vegetation cover were documented for each plot:

- Total cover of phanerogams [%]
- Mean vegetation height [cm]
- Estimated cover [%] of each species (living and standing dead parts separately)
- Phenology

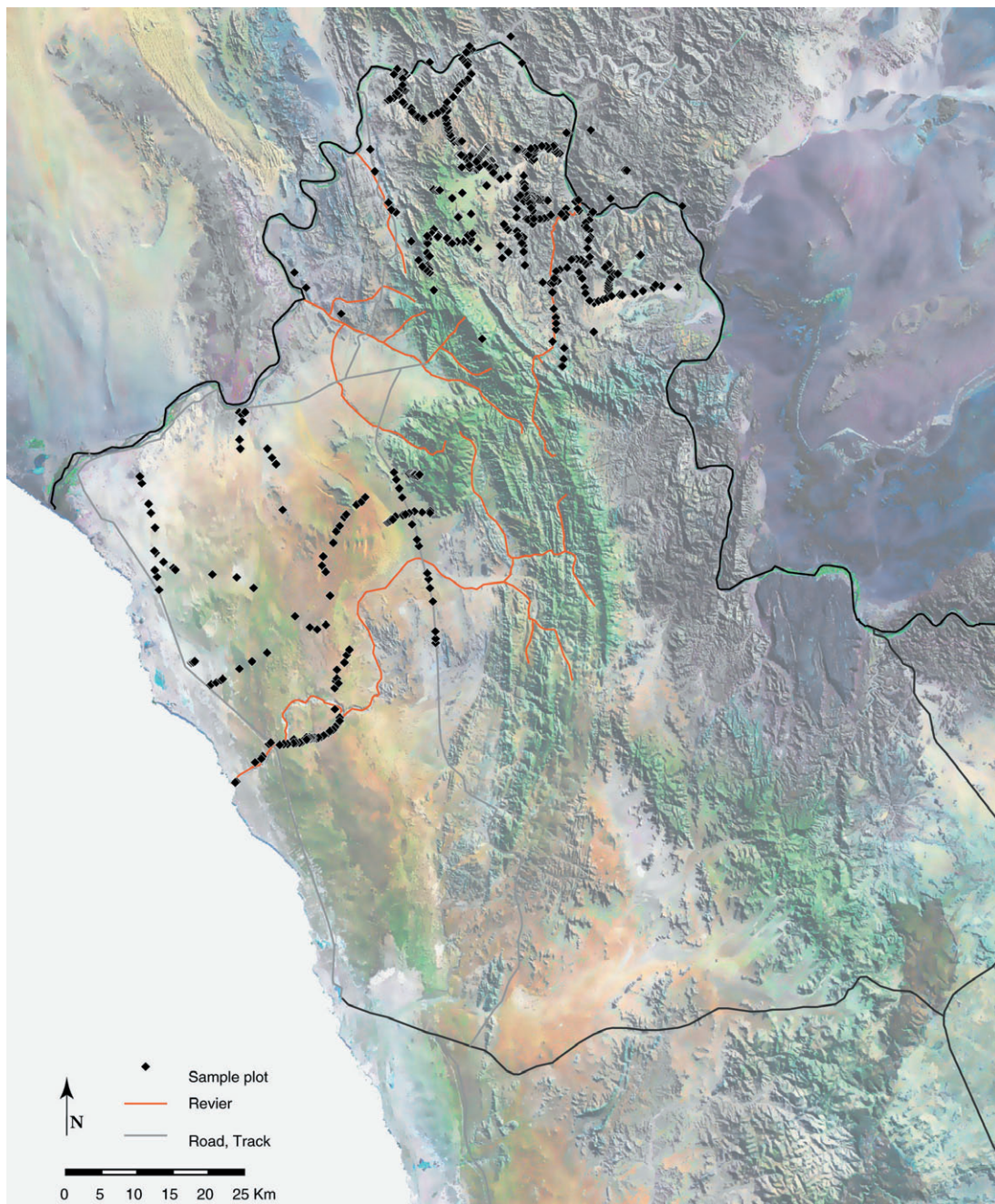


Fig. 2.1: Distribution of the relevés (points) within the study area, northern Richtersveld (total 871 relevés).

### *Vouchers*

For each species, herbarium or living plant specimens were collected and photographs were taken. Additionally, fruits were collected separately for the species of the families Mesembryanthemaceae and Aizoaceae, for identification purposes. The vouchers are lodged at the Herbarium of the South African National Parks in Kimberley (SANP, RSA), at the Herbarium of the McGregor Museum in Kimberley (KMG, Nature Conservation, Northern Cape Province, RSA) and at the Herbarium Hamburgense (HGB) of the University of Hamburg (BRD). The living plants were given to the greenhouse collection of the Botanical Garden at the University of Hamburg for cultivation.

## **2.2. Plant identification, taxonomy and nomenclature**

### *Identification*

The identification of the species took place in the Compton Herbarium (NBG) at the National Botanical Institute (NBI) in Cape Town and at the Nature Conservation in Stellenbosch, where A. le Roux initiated a large collection of Namaqualand species. Additionally, species of the genera *Ruschia*, *Antimima* and *Drosanthemum* were compared with the type specimens of the Bolus Herbarium, University of Cape Town (UCT), investigated by H. Hartmann (Botanical Institute, University of Hamburg). Where necessary, specialists were consulted in the Herbarium. Literature used for the identification of vascular plants was mainly Merxmüller (1972), Le Roux & Boucher (1993), and Le Roux & Schelpe (1988).

Other more detailed treatments used were: Poaceae: Gibbs Russell et al. (1990), Aizoaceae: Hartmann (2002), Hartmann & Stüber (1993), *Psilocaulon*: Klak & Linder (1998), *Brownanthus*: Pierce & Gerbaulet (1997), *Drosanthemum*: Bruckmann (1997), *Cheiridopsis*: Hartmann (1987), *Leipoldtia*: Hartmann (1994), *Eberlanzia*: Hartmann (1993), *Antimima*: Hartmann (1998), *Ruschia*: Hartmann (1998), *Cephalophyllum*: Hartmann (1988), *Jordanniella*: Hartmann (1984), *Conophytum*: Hammer (1993), *Pelargonium*: Van der Walt (1977), Van der Walt & Vorster (1981), (1988), *Trachyandra*: Manning (1990), *Zygophyllum*: Van Zyl (2000) and trees: Palgrave (1993) and Wyk (1997).

### *Nomenclature*

The nomenclature follows the species list PRECIS (Botanical Research Institute Herbarium Data Bank) of the National Botanical Institute (Cape Town), which was published in June 2000 with the program Turbowin (Hennekens 2000). The Illustrated Handbook of Succulent Plants (Hartmann 2002) was used as the nomenclature base for the Aizoaceae, which will be added to the PRECIS species list. The nomenclature of the family follows Brummit (1992).

Several species were not identified. These species are named with 'genspec'. In some cases the family, in others the genus, have been correctly classified. The number behind the 'genspec' or behind the taxa is the sampling number (FNR). If there is a number provided with only four figures it is the number of the film and slide. The term 'species' follows the taxa when species that were not sampled, could only be named by the genus. If species are not described they are indicated with the term 'species nov.'. The shortcuts for e.g. sub-species within the taxa (according to the species list PRECIS, Hennekens 2000) are provided in the abbreviations table A. 1. A comprehensive species list of the northern Richtersveld is shown in table A. 12.

*Eberlanzia ebracteata*

*E. ebracteata\_coast* and *E. ebracteata\_inland* are two variants of the species *E. ebracteata*. *E. ebracteata\_coast* occurs on the coastal plain and *E. ebracteata\_inland* appears on the silty plains within the mountain region. These variants differ in their shape and their colour. *E. ebracteata\_coast* has a more creeping shape and its leaves are more blue-green. The shape of *E. ebracteata\_inland* is ascending and the leaves are yellow-green.

*Antimima* S. *Clavipes\_kahn*

This species is not described. The term 'kahn' after the Subgenus *Clavipes* describes the shape of the leaf according to the German word 'kahnförmig'. That means: shaped like a small boat. This name was given by N. Jürgens.

*Eberlanzia sedoides\_big* blue-green

*E. sedoides\_big* blue-green is a variant of the species *E. sedoides* and differs from the latter in size and colour.

*Euphorbia mauritanica\_Gariep*

The drought-deciduous *Euphorbia mauritanica* varies from a dwarf (approx. 16 cm high) variant *corallothamnus* near Alexander Bay, to a 130 cm high var. *mauritanica* distributed throughout the Sandveld. The common form of the Richtersveld Mountain District is called var. *foetens*. The variant 'Gariep' occurs only in the eastern Gariep and has narrow axes that are reddish on their tips (Williamson 2000).

*Lampranthus \_6* valves

Due to its habit this species belongs to the genus *Lampranthus*, but the fruit capsule has 6 instead of the 5 valves that are typical for this genus. Identification was not possible.

*Leipoldtia\_Numees*

This *Leipoldtia* species only occurs in the Numees region and could not be identified.

*Psilocaulon dinteri\_inland*

This variant of *Psilocaulon dinteri* that occurs further inland on the coastal plain has narrower leaves and reaches heights of over 1 m.

*Psilocaulon salicornioides\_creeping*

The species *Psilocaulon salicornioides\_creeping* has the same appearance as *P. salicornioides* but it is a creeper. Identification was not possible.

*Ruschia Sarmentosa\_ascending fruits*

The ascending fruits are typical for this *Ruschia* of the group *Sarmentosa*. The fruit axes are unusually long and the fruit inflorescences protrude from the plant. The species could not be identified.

*Ruschia Tumidula\_black fruits*

The black capsules are obvious for this *Ruschia* of the group *Tumidula*. Another variant of this species has the same appearance but it is a creeper: *Ruschia Tumidula\_black fruits* creeping. Both could not be identified.

*Zygophyllum cordifolium\_fine*

The species *Zygophyllum cordifolium\_fine* resembles the species *Zygophyllum cordifolium* but its height is lower and the habit is more delicate. Identification was not possible.

*Growth form*

Each species was classified into a growth form category based on the species' life form *sensu* Raunkiaer (1907, elaborated by Orshan 1953, Ellenberg & Mueller-Dombois 1967, Barkman 1988). Raunkiaer's life forms were enlarged by Jürgens growth form concept (1986, 1990). His concept is suited to the special characteristics of the succulent dwarf shrub formation. At first the chamaephytes and phanerophytes were further subdivided as follows and some special features of the stems and leaves were added:

T	Therophytes	
G	Geophytes	
H	Hemicryptophytes	
Ch	Chamaephytes	
NCh	Nano-chamaephytes	0 - 5 cm
MiCh	Micro-chamaephytes	5 - 15 cm
MCh	Meso- to Mega-chamaephytes	15 - 50 cm
P	Phanerophytes	
NP	Nano-phanerophytes	0.5 - 2 m
MiP	Micro-phanerophytes	2 - 5 m
MP	Mega-phanerophytes	> 5 m

s	stem	s rept	creeping
		s rut	switch-shaped
		s frut	woody
s su	stem succulent	s su lept	slender
		s su pach	thick
l	leaf	l ann	deciduous
		l per	evergreen
		l nan	dwarf-form
		l red	reduced
l su	leaf succulent	l su ann	deciduous
		l su per	evergreen
		l su nan	dwarf-form
		l su red	reduced
r su	root succulent		
th	thorny		

### *Species distribution*

The remarks on the distribution area of the most important species are taken from Arnold (1993).

## **2.3. Chemical and physical soil analysis**

The majority of the 377 soil samples were taken as mixed samples from the first 10 cm avoiding the surface until 1 cm below. Soils from the plains, that showed a weak differentiation in layers, were sampled in more detail, depending on the number of obvious layers. For every soil sample the following soil data were collected (A. 13):

- Stone content (> 2 mm in diameter) in soil [%].
- The thickness of the fine material above the bed rock or crust [cm].
- Limiting layer of the horizon (bed rock, different sort of crust).
- Carbonate content (semi-quantitative) by employing the standardised HCl-test outlined in soil survey standards (*Bodenkartieranleitung*, AG Boden 1994).
- Electrical conductivity determined in a 1:5 suspension of air-dry fine material and aqua bides employing the WTW LF 91 instrument.
- Soil pH in a 1:25 suspension of air-dry fine material and aqua bides (4 g soil/10 ml aqua bides) and 0.1 M CaCl<sub>2</sub>. After one hour the suspensions were measured by using a WTW Digital pH-meter.

The soil colour was identified in a moist condition outlined in the Munsell Soil Colour Charts (1994). The profiles of the plain soils were described and the soil texture deter-



mined by employing the standardised finger test outlined in the soil survey standards (*Bodenkartieranleitung*, AG Boden 1994).

Furthermore the ground cover of physical and microbiotic crusts were estimated, as well as the amount of phytogenic mounds (PGM) and drown axis [%]. Both, the first and the latter parameters enable the opportunity to assess the present erosion and/or accumulation processes. Phytogenic mounds develop when surface material is eroded by water or wind. The surface material around the perennial plant is held by its roots and forms the mound whereas wind or water removes the surface material, which is not covered by plants. Where sediment accumulates, the axis of the plant becomes covered (drown axis).

The soil texture, of altogether 21 soil samples, was analysed by M. Facklam from the Institute of Ecology (Soil Science Dept.) at the Technical University, Berlin.

The content and composition of the most relevant soluble salts for plants were determined for 149 relevés. The anions chloride, nitrite, nitrate, phosphate and sulphate and the cations sodium, ammonium, potassium, magnesium and calcium were determined.

The preparation of the samples complied with the standard of the Institute of Soil Science, University of Hamburg, which is used for desert soils. This process follows the method of Rhoades (1996). A suspension of 25 g air-dry fine material (< 2 mm) and 25 ml aqua bides was shaken for 1 h, centrifuged at 3000 U/min for 25 min and filtered. The filtered suspension was diluted 1:10. The anions and cations were measured using an ion-chromatography instrument (Dionex DX 120). Eluents were a 22 M  $\text{H}_2\text{SO}_4$  for the cations and a 3.5 M  $\text{Na}_2\text{CO}_3$  / 1.0 M  $\text{NaHCO}_3$  for the anions.

## **2.4. Derivation of additional explanatory variables**

Several parameters, which could not be reliably measured in the field, were prepared in order to aid in the assessment of ecological variables as predictors for community patterns in the classification and ordination analyses. These data and models were kindly provided by F. Darius and A. Bolten (ACACIA/E1, University of Cologne).

### **2.4.1. Satellite remote sensing datasets**

Two multispectral (14 bands) images of the study area were acquired, each covering 61.5 by 63 km. The data were recorded by the ASTER sensor on-board the NASA's Terra satellite (Yamaguchi et al. 1998) and enable the extraction of a digital elevation model (DEM) from two along-track stereo images. The dataset was acquired as orbit-oriented level 1A data with a 15-m spatial resolution. In order to set up the satellite image base map, the three visible/near-infrared bands (1/2/3N) were de-striped, orthorectified, and combined with the DEM extracted from the 3N/3B bands using PCI Geomatics' OrthoEngine. The resulting image was colour enhanced and georeferenced with selected

ground control points from the field data. Topographic features for each sampling location, such as elevation, slope, and aspect were derived using the standard modules of a GIS package (ESRI) from the DEM dataset.

**2.4.2. Climatic variables**

Due to the scarcity of long-term weather observations within the study area, climatic data were derived by interpolation from surrounding station records. The source database was the global mean monthly climatology for the period 1931-1960 (Cramer & Leemans 1999). It contains long term monthly averages of mean temperature (TMEAN), temperature range (TRAN), precipitation (PREC), rain days (RD), and percent sunshine of potential hours (SUN), gridded at 0.5 degree longitude/latitude resolution. The station data were interpolated using thin-plate splines explicitly incorporating elevation as a predictor variable. After calculation of mean minimum and maximum temperature (TMIN and TMAX, respectively) this database was further extended by the addition of seasonal averages (w = June to August, s = December to February) and annual averages (or totals: PREC, RD). A subset of this database was re-gridded to a resolution of 0.05 degree within 27°S to 31°S and 16°E to 21°E using an inverse distance weighted least squares method as implemented by the Surfer 8 software package (Golden Software, Inc.). The values of all the variables' surfaces at each field sampling coordinate were obtained and assigned to the respective plot record.

**2.5. Classification and ordination of the vegetation data**

*Syntaxonomic work*

The vegetation classification presented in this study is based on the comparison of quantitative vegetation data by means of vegetation tables. The subdivision of 871 plots into five different tables according to the main landscape units was established by a hierarchical cluster analysis (see below). The five tables have been pre-sorted with TWINSpan (Hill 1979). All default settings were chosen except for the cut levels (see below).

The ground cover was estimated for each species as a percent-value of the plot surface. These values were entered into the database (MS Access). For the pre-sorting of the five tables in TWINSpan the values were transformed to a 1 - 9 scale according to Van der Maarel (1979), using appropriate cut levels.

The scale is related to the Tüxen & Ellenberg (1937) average cover percent scale (left) as follows (approximation after Van der Maarel (1979), right):

Scale	% Cover	Cut level	% Cover
1:	= 0.02	1:	< 0.06
2:	= 0.1	2:	< 1.3

3:	=	2.5	3:	<	3.75
4:	=	5.0	4:	<	6.875
5:	=	8.75	5:	<	13.75
6:	=	18.75	6:	<	28.125
7:	=	37.5	7:	<	50
8:	=	62.5	8:	<	75
9:	=	87.5	9:	≤	100

After the pre-sorting the values were re-transformed to the percentage values.

Several relevé characteristics were added to the head of the table:

Species richness (S):	SPEC [n]
Total ground cover:	COV/10 = cover [%] / 10
Shannon diversity index	H-INDEX $H = - \sum_i p_i \ln(p_i)$ , ( $i = 1, 2, 3, \dots, S$ ), $0 \leq H' \leq \infty$
Pielou's evenness index:	EVENESS $E = H' / \ln(S) = - \sum_i p_i \ln(p_i) / \ln(S)$
Distance to the coast:	DIST/10 = distance [km] / 10
Elevation:	ALT/100 = altitude [m] / 100
Inclination:	INCL/10 = inclination [°] / 10
Exposition:	EAST = eastness [E, _, W] NORTH = northness [N, _, S]
Geological unit:	GEO
	(after Villiers & Söhnges 1959)
G00	Quaternary sediments
G01	Coarse grained porphyritic granite (Tatasberg Complex and Kuboos Pluton)
G02	Medium grained non-porphyritic granite (Tatasberg Complex and Kuboos Pluton)
G03	Ultra-metamorphosed mafic lava (Violsdrif Suite)
G04	Light coloured schist (Orange River Group)
G05	Dark coloured schist (Orange River Group)
G06	Mafic lava (Orange River Group)
G07	Quartzite, conglomerate, meta-quartzite, magnetite rich bands (Orange River Group)
G08	Gray, gneissic granite (Violsdrif Suite)
G09	Ultra-metamorphosed sediment (Violsdrif Suite)
G10	Sheared greywacke and arkose (Schist) (Gariiep Complex)
G11	Quartzite and sandstone (Stinkfontein Formation)
G12	Tillite with lenses of shale and dolomite (Gariiep Complex)

The theoretical background of the Braun-Blanquet approach in this study has been laid out in the literature (Braun-Blanquet 1928, 1951, Ellenberg 1956, Mueller-Dombois & Ellenberg 1974, Dierschke 1994). Nevertheless, some important remarks as to its use in this study will be given here.

The aim of the comparative work with the tables is to find out species groups or communities that repeatedly occur together, that have a similar ecological potency and/or have a similar distribution area.

In this context, community refers to any vegetation unit that has distinctive characters and homogeneity (Willard 1979), without any implications as to its hierarchical classification. The comparison of different communities and the assessment of their rank lead to a hierarchical system. This process of classification is the aim of this study.

The hierarchical Braun-Blanquet system is ordered with class as the highest level, then order, alliance, association, sub-association and variant. These syntaxa are characterised by diagnostic species (differential species or character species). The diagnostic species were defined here as follows:

A differential species is one, which only occurs in one syntaxon of a particular hierarchical level and is, by definition, absent or rare in the other syntaxa of this level.

A character species is a special case of a differential species. It occurs only in one syntaxon and is absent in the whole hierarchical system.

Diagnostic species reach constancy values between 40 and 60 % within the table. The constancy value is a measure for the presence of a species in a given community. It is a synthetic character of plant communities and is mainly used in synoptic tables in order to compare vegetation units. The following scale of constancy has been used in this study (Dierschke 1994):

V	>	80 - 100 %	I	>	10 - 20 %
IV	>	60 - 80 %	+	>	5 - 10 %
III	>	40 - 60 %	r	>	- 5 %
II	>	20 - 40 %			

Diagnostic species of high diagnostic value have constancy classes of III - V within the vegetation unit and are lacking outside the unit. As a rule, diagnostic species should occur with constancy classes of III - V within the unit and with two classes lower outside:

V / IV	-	II, I, +, r, 0
III	-	I, +, r, 0

The association, the basic unit of the hierarchical Braun-Blanquet system, is defined by at least two diagnostic species and furthermore by a characteristic species combination. The name of the given association consists of the two main character species if available. The association is, in this study, subdivided into sub-associations if floristic aspects show unremarkable deviation within the association caused by ecological, geographical or topographical differences. Unlike the association, a separation by differential species is sufficient. If the associations show a set of additional species due to varying habitat

conditions, this sub-association is named by its characteristic species. The typical prevailing section of the association, excluding the additional species, is called a 'typicum' sub-association (Koch 1926).

The alliances are groups of similar associations sharing a number of diagnostic species and having similar ecological characters. The name of these alliances also consists of the two main character species.

#### Notes to the classification in this study (see also the discussion, chapter 4)

Several problems arose with the process of classification. The aim of this study was to rank the plant communities found. Within the lower syntaxa levels the results are satisfactory, whereas for the higher levels the division becomes increasingly uncertain due to the fact that a general phytosociological system for the western coast does not exist. Details regarding order or alliance are preliminary in this study - classes are not provided. For this reason a nomenclature, which follows the strict procedure of the Code of Phytosociological Nomenclature (Weber et al. 2000) was not applied. The name of the syntaxa is focused on ecological, topographical and physiognomic aspects and consists of two diagnostic species (potential character species, see below).

The definition of character species is impossible due to the previously mentioned circumstances. Therefore the distinction of character and differential species is omitted and a general statement of diagnostic species is provided in the head of the community description (see below). Underlined species are potential character species.

Some associations have no potential character species and only one or no differential species in regions where species number and canopy cover are low. The rank of these syntaxa is therefore uncertain with regard to the Braun-Blanquet system.

In this syntaxonomic work only typical relevés enter the classification, relevés showing transitions between syntaxons were eliminated. The elimination of untypical relevés is a normal part of every phytosociological analysis based on types. The subjectivity of this process is criticised, but this criticism misjudges the background of the scientific forming of types (Tüxen 1974). Braun-Blanquet (1955) demands ten typical relevés for a syntaxonomic assessment, which is nearly guaranteed for every association in this study. In a second step untypical relevés were assigned to the types found, which are accessible via database for further studies.

#### Synoptic table

The synoptic table gives the combined results of all five differentiated tables. It is the main tool for the development and definition of the higher units of the syntaxonomic system. Synoptic tables show the species in rows, whereas the vegetation units are arranged as columns next to each other. Each column represents one or a number of relevés belonging to the unit. In the latter case, the data has been condensed into a presence/absence-calculated constancy class. The mean ground cover [%] of the species

within the vegetation unit is given in a small number after the constancy classes. Mean number of species and mean ground cover [%] of the vegetation units are given in the head of the synoptic table. Life form and chorotype are added to the right for every diagnostic species. Only species occurring with low constancy or in a few units have been omitted from the synoptic table.

### Community descriptions

The head of the description consists of the preliminary name. Then a list of the plots from the study area follows. Next, the diagnostic species are listed in approximate order of importance (including exclusiveness and constancy). Underlined species are potential character species, the others are potential differential species (see above). Finally the constant companions are listed, if available.

The description of all vegetation units is structured as follows.

A brief physiognomic description with reference to special features of the unit. Information on the topographical situation including ecologically important factors: relief, landscape, exposition, inclination, and elevation range. Notes on the geology and a brief description of the soil properties. Common notes on the climatic situation: macro-/micro-climate.

Special floristic features of the unit are given: floristic composition and differentiation as well as vegetation structure and patterns are mentioned. The distribution of the main diagnostic species is given where accessible. The details of the distribution areas follow the 'Plants of southern Africa, names and distribution' (Arnold 1993). The occurrence of the unit in the study area is given, based on the samples taken and observations made in the area during fieldwork.

### *Cluster analysis*

To reveal the basic structure of the data set a cluster analysis was done, which defines groups of items based on their similarities. The method chosen arranges the groups into a hierarchical system, where the importance of a particular difference decreases from the highest to the lowest hierarchical level. The results are presented in a dendrogram.

All relevés were entered into the analysis, except the continuous micro-transects of the Koeroegabvlakte and the Sandveld. These transects were sampled to document certain microscale structures of the stands. They are not subject of the study and were therefore omitted from further analyses.

The following steps were run to prepare the data set for analyses:

Species that occurred in less than 2 % of the data set were discarded. All data were log-transformed to normalise the skewed frequency distribution of cover values. This also gives more weight to qualitative aspects of the data and therefore less weight to dominant species (Jongmann et al. 1995). The cover values were transformed to binary values

with respect to the sample mean. This transformation emphasises the optimal parts of a species range and also equalises, to some extent, the weight given to rare and dominant species (McCune & Mefford 1999).

The distance matrix was calculated using the Sørensen coefficient (i.e. Bray-Curtis). It is useful for ecological community data, because it retains sensitivity in more heterogeneous data sets and gives less weight to outliers, compared to the Euclidean distance (Legendre & Legendre 1998). Sørensen distance is incompatible with clustering strategies that recalculate inter-group distances such as Euclidian, e.g. the Ward Method. The Ward Method is successfully used for ecological data, but the problem with heterogeneous community data, such as the data under study, is a large number of zeros in the data matrix. Therefore the Flexible beta method, which is compatible with Sørensen distance, was used as the classification method with  $\beta = -0.5$  (Legendre & Legendre 1998). The program PC-ORD 4.0 (McCune & Mefford 1999) was used for these calculations.

The main groups, found by the cluster analysis, formed the basis for the syntaxonomic work within five tables (see above).

### *Ordination*

While the cluster analysis reveals basic structures within the data set, phytosociological classification and ordination should lead to a further detailed interpretation. The phytosociological analysis focuses on the relevés with the most diagnostic value for the classification process, given in the differential tables. These relevé data were used for further descriptive investigations, such as different gradient analyses. The aim of these analyses is to uncover the main factors, which are responsible for the patterns of species composition and distribution.

For this ecological assessment the following explanatory variables were used:

- Climatic factors (as defined in 2.4.2)
- Soil properties
- Exposition
- Inclination
- Elevation
- Geological units

Quantitative variables were standardised to zero mean and unit variance, soil carbonate and conductivity were additionally log-transformed. Nominal data such as geological units were coded to binary variables.

Correlation among variables were checked by calculating the Spearman's rank correlation coefficient. With the inclusion of too many variables distortions may appear in the ordination (Ter Braak 1998). Therefore the non-correlating variables were passed to the Forward Selection module of CANOCO for Windows 4.0 (Ter Braak 1998) in order to reduce the number of variables. Variables that reached a significance of  $p \leq$

0.005 were used as explanatory variables for the ordination analyses. The results are given as tables together with the biplot representation of the CCA.

The relevé data were initially log-transformed before being entered into the different ordination analyses in order to reduce the high variation and to normalise the skewed frequency distribution of cover values within the data set.

The ordinations were run using PC-ORD 4.0 (McCune & Mefford 1999), CANOCO for Windows 4.0 (Ter Braak 1998) and SYSTAT 8.0 at the Institute for Ecology (Botany Dept.), Technical University, Berlin.

### *Indirect gradient analyses*

#### Detrended Correspondence Analysis (DCA)

The detrended correspondence analysis (Hill and Gauch 1980) is an eigenanalysis ordination technique based on reciprocal averaging (Hill 1973) or correspondence analysis (McCune & Mefford 1999). DCA ordines both species and samples simultaneously and uses a chi-squared distance measure.

The following options were selected:

- down weighting of rare species
- rescale axes to unit variance
- rescaling threshold: the default value (0)
- number of segments: the default value (26)

The result of the DCA is shown in a joint plot. After completing the DCA analysis, which is performed on the species data alone, the ordination sources are related to the environmental variables. The angle and length of the arrow show the direction and strength of the relationship.

#### Principal Components Analysis (PCA)

Principal components analysis, the basic eigenanalysis technique, has had many applications in ecology since Goodall (1954). It implicitly uses the Euclidean distance measure (Legendre & Gallagher 2001) and assumes a linear relationship between species abundance and environmental gradients. Because this inhomogeneous data set contains a large number of zeros, which causes problems with the Euclidean distance, the Beals smoothing was used (Beals 1984, McCune 1994). It replaces presence/absence data with quantitative values that represent the „favourability“ of each sample for each species.

$$b_{ij} = 1/S_i * \sum_k (M_{jk}/N_k)$$

$S_i$  - species number in sample  $i$

$M_{jk}$  - number of samples with both species  $j$  and  $k$

$N_k$  - number of samples with species  $k$

The result of the PCA is shown in a joint plot.



---

### *Direct gradient analysis*

#### Canonical Correspondence Analysis (CCA)

Canonical correspondence analysis (Ter Braak 1984, 1994) is attractive for community ecology because it constrains the ordination of samples and species by their relationships to measured environmental variables, which in turn facilitates interpretation. CCA is implicitly based on the chi-squared distance measure that gives a high weighting to species whose total abundance in the data matrix is low. Therefore rare species (< 5 %) were excluded from the data set before analysis. All cover values in the data matrix were log-transformed.

The following options were chosen when running CCA:

- Row and column scores standardised by centring and normalising (gives biplot scaling where site scores are rescaled such that the mean is zero and the variance is one).
- Scaling of ordination scores so that species scores are weighted mean site scores; this choice allows a direct spatial interpretation of the relationship between environmental and species points.

The result of the CCA is shown in a biplot. The resulting ordination is a product of the variability of the environmental data and the variability of the species data. Both quadrat scores and species are plotted on the same graph but using different scales (see above). The angle and length of the arrow show the direction and strength of the relationship between the ordination scores and the environmental variables.

#### Side scatter plots

Variables in the main matrix (quantitative) or in the second matrix (quantitative or categorical) can be used as ordination overlays (McCune & Mefford 1999). Graphic overlays of quantitative variables are convenient for relating individual variables to the ordination space. Categorical variables are used as overlays by coding with colours or symbols.

Two components are shown in the output:

An ordination diagram, where the ordination points have been replaced by various sized symbols, the size being proportional to the size of the variable.

Two additional scatterplots are shown besides the ordination overlay. The scatterplot below the ordination relates the overlay variable (vertical axis) to the horizontal axis of the ordination. The scatterplot to the left of the ordination relates the overlay variable (horizontal axis) to the vertical axis of the ordination. An envelope that includes about 95 % of the points is included. The scale of the y-axis shows the abundance of the species and the scale of the x-axis represents the ordination scores of the CCA.

## **2.6. Vegetation mapping**

The production of the vegetation map was accomplished within a GIS environment. The work based primarily on a high resolution, orthorectified false-colour satellite image (ASTER) and several intermediate map products derived from a 30-m resolution digital elevation model. Digital terrain data, such as contour lines, slope angle, orientation, and drainage net, has been used in combination with spectral data to identify the areas where a certain vegetation type or syntaxon is assumed to be dominant or representative. Overlays with geological information, obtained from the digitised map of Villiers & Söhnge (1959), also proved to be helpful in delineating the vegetation units. In order to preserve the readability of the resulting map, syntaxa defined exclusively by different slope aspects were disregarded.

### 3. Results

The vegetation of the Richtersveld was investigated along a coast-inland transect of 881 relevés. The map in Fig. 2.1 shows the distribution of the relevés within the study area. The subdivision of the relevés into the four main landscape units, coastal plain (Sandveld), silty plains and basins (vlakke), mountain area, separated into Succulent Karoo and Nama Karoo, and gravelly flood plains and drainage lines, is given in Fig. 3.1.

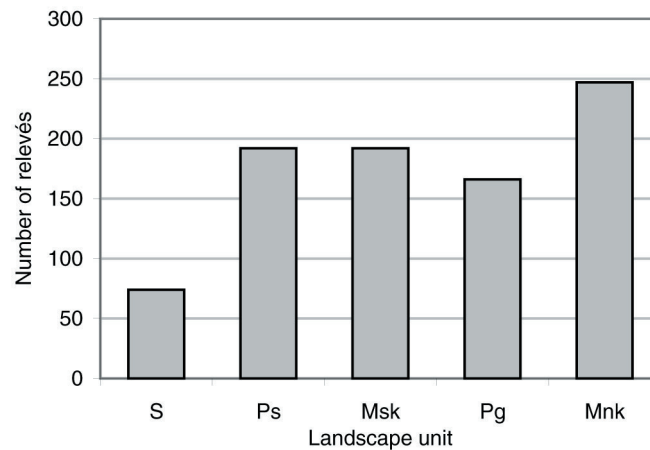


Fig. 3.1: Distribution of the relevés within the five basic landscape units. Abbreviations: S = Sandveld (coastal plain); Ps = silty plains; Pg = gravelly plains; Msk = mountain slopes within the Succulent Karoo and Mnk = mountain slopes within the Nama Karoo.

#### 3.1. Classification

In the following chapter the conclusions of the syntaxonomic work is shown. First the main structure of the sampled relevé data in different vegetation tables is introduced. The results of the cluster analysis will be compared with the observations made in the area during the fieldwork (section 3.1.1.). Secondly the preliminary classification, as a consequence of the differentiated vegetation tables and the synoptic table, is presented (section 3.1.2.) with a detailed description of the vegetation units.

##### 3.1.1. Cluster analysis

The intention of the cluster analysis was to find the main groups from the complete vegetation data ascertained for the phytosociological study. The cluster analysis was run on all life forms, geophytes, hemicryptophytes, phanerophytes, chamaephytes and therophytes.

Interpretation of the hierarchical cluster analysis reveals that five groups are recognized at levels three and four (Fig. 3.2). These are the dwarf shrub-land on sandy habitats of the coastal plain, the dwarf shrub-land on silty habitats of the coastal plain and inner-mountain basins, the dwarf shrub-land on silty slope habitats of the mountain area, the dry shrub-land on silty slope habitats of the mountain area and the shrub-land on gravelly

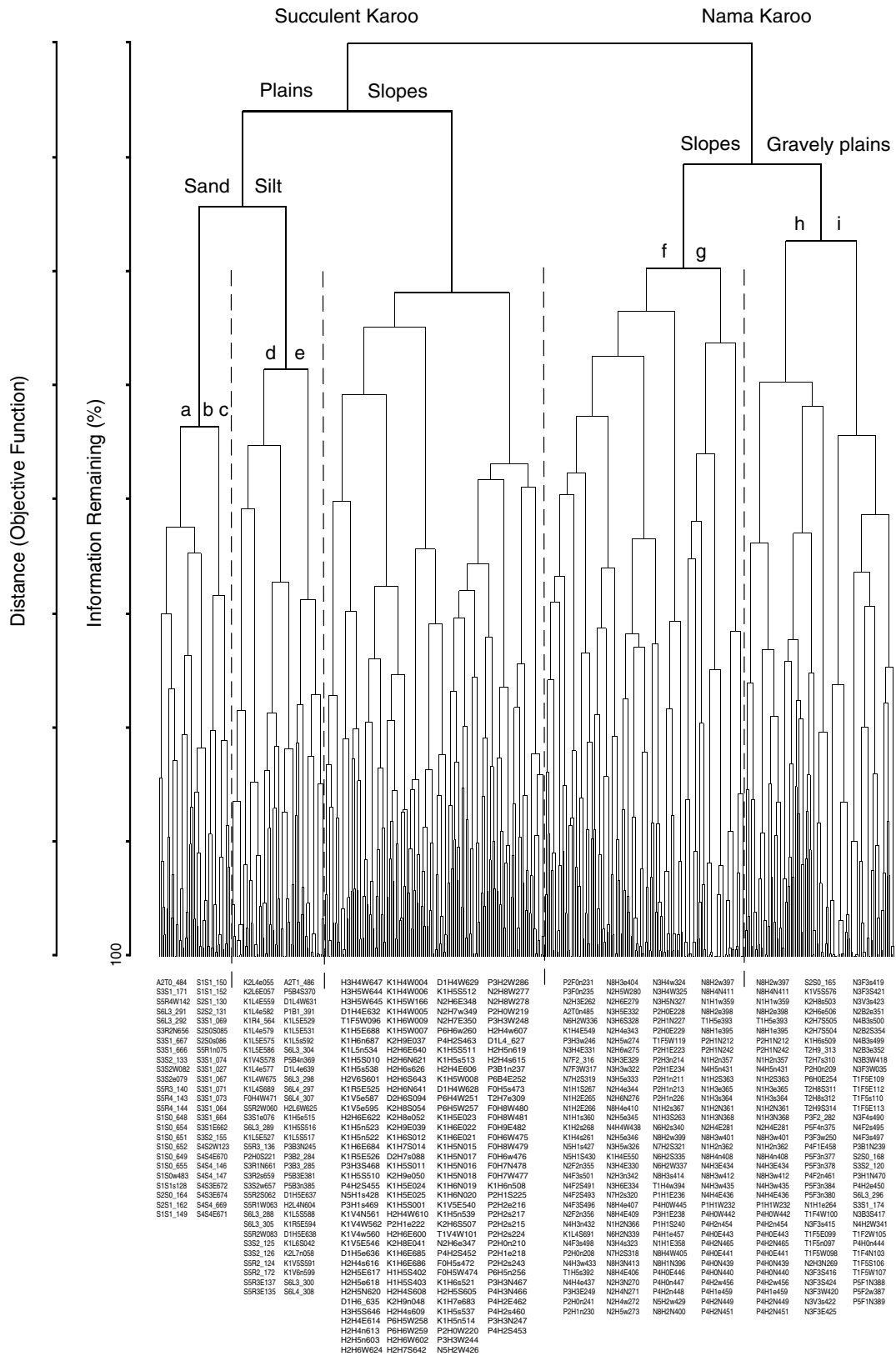


Fig. 3.2: The result of the hierarchical cluster analysis [Sørensen index, Flexible beta : -0.5] on the basis of 515 relevés and 403 species, is shown in the dendrogram (overview). The first y-axis gives the distance (Objective Function) of the levels and the second y-axis gives the remaining information [%]. The plots are arranged along the x-axis.

plains and drainage lines of the inner-mountain basins and valleys. The dwarf shrub-land formation is part of the Succulent Karoo whereas the dry shrub-land formation is part of the Nama Karoo. The first level of the hierarchical cluster analysis shows a floristic division in the two kingdoms *Greater Cape Flora* with the Succulent Karoo Region and *Palaeotropis* with the Nama Karoo Region. The following divisions are based on ecological features. On the second and third level the plains are separated from the slope habitats due to exposition and inclination differences. Whereas the vegetation of the plains mainly depends on soil properties which leads to the fourth division.

The lower levels reveal some significant divisions (A. T1). Within the group of sandy habitats the relevés of the coastline with white sand (a), the inner-coastal plain with red sand and the red dune (b, c) are recognized (Fig. 3.2). The silty plains are subdivided into the habitats of the coastline and the inner-mountain basins (d, e). The more diverse plots are separated from the species-poor plots directly at the dry Orange River valley within the slope habitats of the Nama Karoo (f, g). Within the group of gravelly plains the relevés of the drainage lines in the western part of the Richtersveld are significantly split from those of flood plains and drainage lines in the eastern part (h, i).

The division within the slope habitats of the Succulent Karoo is un-satisfactory. Just as the assignment of the relevés on the south exposed slopes to the group of gravelly plains is controversial. These facts and the weak resolution of the division on the lower level of the hierarchical cluster analysis provides a reason to order the data set in detail within vegetation tables following the syntaxonomic system of Braun-Blanquet. The five main groups of the hierarchical cluster analysis correspond with the number of vegetation tables.

Relevés which are not optimally assigned to one of the main groups were taken off and joined to another if it made sense. For example, the plots of south exposed slopes were put into the table of slope habitats of the Succulent Karoo.

(Fig. 3.2, cont.)

*The division of the vegetation into the five basic groups according to the landscape units is indicated at the second and third level. The division for lower levels: a = white sand habitats; b = red sand habitats and c = red dune habitat on the sandy coastal plain; d = silty plain habitats of the coastal plain and e = silty plain habitats of the inner-mountain basins; f = more diverse slope habitats and g = species poor habitats within the Nama Karoo; h = Succulent Karoo- and i = Nama Karoo- species on the gravelly plain habitats of the drainage lines.*

### 3.1.2. Braun-Blanquet approach

#### Introduction to the flora and life forms

The semi-desert vegetation of the Richtersveld shows a high species diversity. Of 1615 known species (Williamson 2000), 622 species were recorded during the fieldwork within the study area. Looking at the five main landscape units, Sandveld (S), silty plains (Ps), mountain slopes of the Succulent Karoo (Msk), mountain slopes of the Nama Karoo (Mnk) and gravelly plains and drainage lines (Pg), the mountain slopes of the Succulent Karoo is, with 393 species, the most diverse landscape unit of the Richtersveld (Fig. 3.3). The species diversity and vegetation cover decreases from the coast further inland. The mean number of species decreases from 20 to 7 and the mean ground cover declines from 20 to 7 % in the same direction (Fig. 3.4).

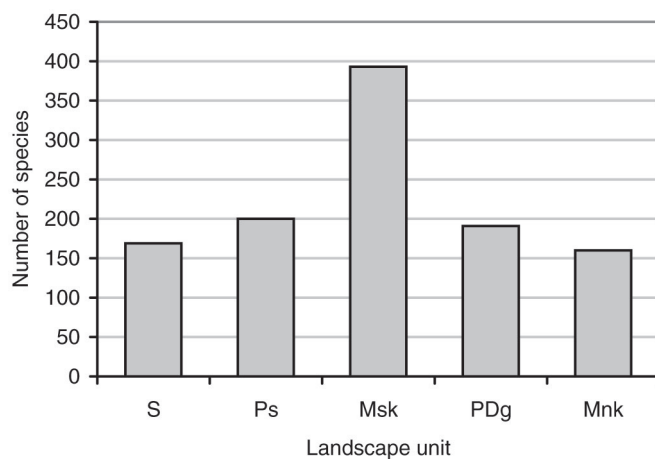


Fig. 3.3: Total species number [n] of the northern Richtersveld landscape units. Abbreviations: S = Sandveld (coastal plain); Ps = silty plains; Pg = gravelly plains; Msk = mountain slopes within the Succulent Karoo and Mnk = mountain slopes within the Nama Karoo.

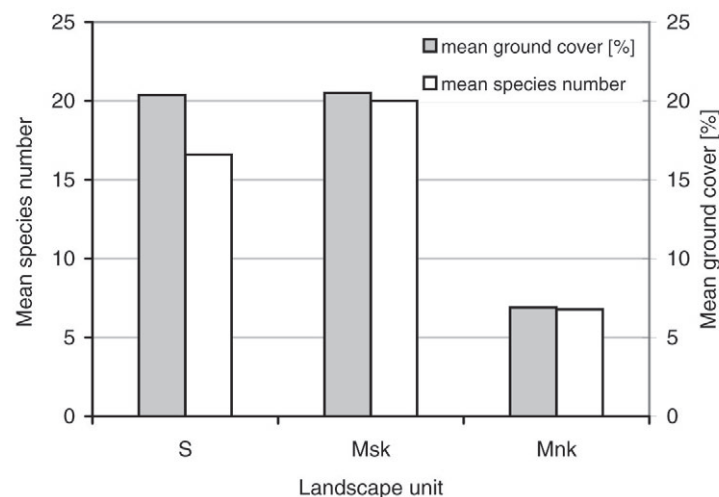


Fig. 3.4: Mean species number [n] and mean ground cover [%] from the coast to the interior along the main climate gradients precipitation and temperature. Abbreviations: S = Sandveld (coastal plain); Msk = mountain slopes within the Succulent Karoo and Mnk = mountain slopes within the Nama Karoo.

The life form spectrum shows the dominance of the chamaephytes (C) with 53 %, followed by the therophytes (T) with 21 % and phanerophytes (P) with 13 % (Fig. 3.5). Hemicryptophytes (H) are represented with 6.7 % and the geophytes (G) with 6.4 %. The amount of chamaephytes decreases from the coast to the eastern Gariep, whereas the phanerophytes increase (Fig. 3.6). Within the study area the western part of the mountain region has 60 % chamaephytes versus 12 % phanerophytes, the eastern part counts 43 % chamaephytes to 33 % phanerophytes. The therophytes reach the highest amount upon the plains (vlaktes).

The same is true for the growth forms leaf succulence and stem succulence. Leaf succulence decreases from the coast to the eastern Gariep (from 44 to 35 %) and the stem succulence increases from 16 to 28 % (Fig. 3.7).

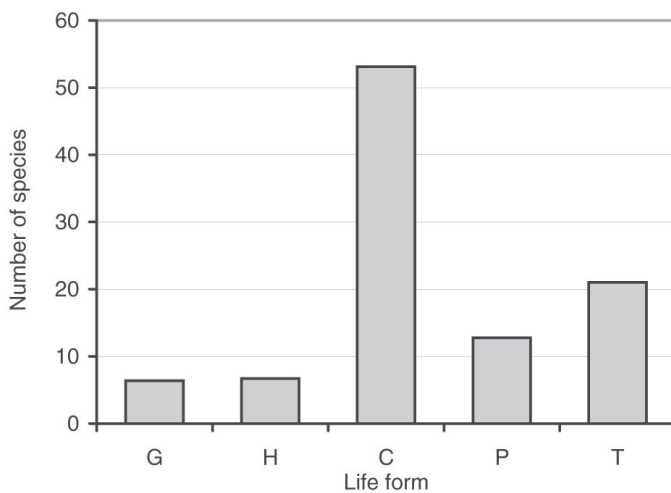


Fig. 3.5: Life form spectrum [%] within the northern Richtersveld. Abbreviations: H = hemicryptophytes; G = geophytes; P = phanerophytes; C = chamaephytes and T = therophytes.

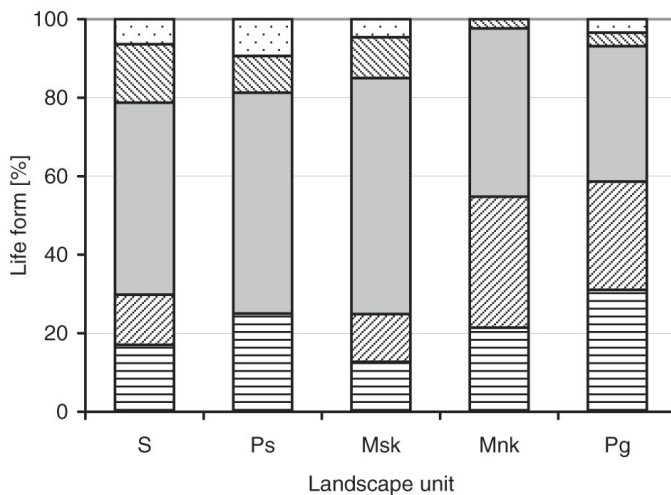


Fig. 3.6: Life form spectra of the northern Richtersveld landscape units [%]. Abbreviations: S = Sandveld (coastal plain); Ps = silty plains; Pg = gravelly plains; Msk = mountain slopes within the Succulent Karoo; Mnk = mountain slopes within the Nama Karoo; H = hemicryptophytes; G = geophytes; P = phanerophytes; C = chamaephytes and T = therophytes.

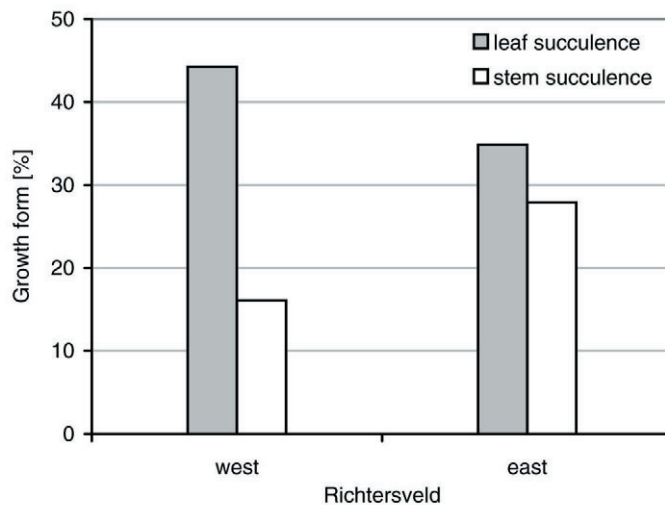


Fig. 3.7: The percentage of two important growth forms, leaf and stem succulents in the western part (Succulent Karoo) and the eastern part (Nama Karoo) of the northern Richtersveld.

### Phytosociological study

The comparative work within the differentiated tables found 22 associations. Two communities are not connected with the classification system, because species are absent, which they share with other syntaxa. Hence these vegetation units on edaphically special habitats are not ordered into the hierarchical system. The 'Stipagrostis obtusa com.' is not connected with the classification, because the data base is not abundant. The order for the higher syntaxa can be taken from the data set of the synoptic table. Classes are not provided due to the fact that a general phytosociological system still does not exist for the western coast of southern Africa (see chapter 2.5 and 4.2). Therefore the division on higher syntaxa level is uncertain and has to be regarded as a preliminary approach. The Succulent Karoo and the Nama Karoo are the two orders with six alliances in total. The detailed structure can be taken from the classification summary given below. The tables, presented in appendix A. T2-7, are discussed in the following section 'Description of the vegetation units'.

### Classification Summary

- 1 Habitats of the Succulent Karoo
  - Order: Tetragonia echinata - Pteronia glabrata ord. prov.
  - 11 Habitats on plains and basins of the Succulent Karoo
    - Sub-order: no diagnostic species
    - 111 Sandy habitats of the coastal plain (Sandveld)
      - Alliance: Eberlanzia ebracteata\_coast - Lebeckia multiflora all. prov.
      - 1111 Habitats on the coastline on white sands
        - Association: Zygophyllum clavatum - Euphorbia brachiata ass. prov.
        - 11111 Firm sand habitats without psammophytes
          - Typicum: Zygophyllum clavatum - Euphorbia brachiata typ. nov.
          - 11112 Habitats on consolidate sand body with psammophytes
            - Sub-association: Othonna sedifolia - Tripteris oppositifolia sub-ass. prov.



- 1112 Habitats of the inner-coastal plain on red sands
  - Association: *Zygophyllum morgsana* - *Hermannia trifurca* ass. prov.
  - 11121 Habitats on red sands
    - Sub-association: *Jordaaniella clavifolia* - *Chaetobromus involucratus* sub-ass. prov.
    - 111211 Habitats on sand sheets and inter-dune sections
      - Variant: *Jordaaniella cuprea* - *Crassula atropurpurea* v. *cultriformis* var. prov.
    - 111212 Habitats on dune crests
      - Variant: *Stoeberia utilis* - *Ruschia Sarmentosa\_ascending* fruits var. prov.
  - 11122 Habitats on the red dune
    - Sub-association: *Cladoraphis spinosa* - *Limeum fenestratum* sub-ass. prov.
  - 11123 Sandy habitats in the zone of high corrasion south of the lower Orange River
    - Sub-association: *Brownanthus arenosus* sub-ass. prov.
- 112 Silty habitats of the coastal plain (Sandveld) and the inner-mountain basins
  - Alliance: *Brownanthus pseudoschlichtianus* - *Drosanthemum inornatum* all. prov.
  - 1121 Silty habitats of the coastal plain
    - Association: *Cheiridopsis robusta* - *Ruschia leucosperma* ass. prov.
  - 1122 Silty habitats of the inner-mountain basins
    - Association: *Aridaria noctiflora* s. *noctiflora* - *Trachyandra muricata* ass. prov.
- 12 Slope habitats of the Succulent Karoo within the mountain area
  - Sub-order: *Tylecodon paniculatus* - *Osteospermum armatum* sub-ord. prov.
  - 121 Seaward habitats of the escarpment ranges
    - Alliance: *Didelta spinosa* - *Helichrysum hebelepis* all. prov.
    - 1211 Summit habitats of the escarpment with Fynbos elements
      - Association: *Galenia africana* - *Prenia pallens* ass. prov.
      - 12111 Summit habitats on high elevation, above 1200 m a.s.l.
        - Sub-association: *Elytropappus rhinocerotis* - *Merxmuellera dura* sub-ass. prov.
      - 12112 Summit habitats on lower elevation, altitude 900 - 1200 m
        - Sub-association: *Pteronia divaricata* - *Berkheya canescens* sub-ass. prov.
    - 1212 Granite habitats of the escarpment annex Goariep mountains; 500 - 900 m
      - Association: *Antizoma miersiana* - *Ruschia Tumidula\_black* fruits ass. prov.
    - 1213 Habitats of the Vandersterrberg - Stinkfonteinberge; 500 - 900 m
      - Association: *Crassula grisea* - *Ruschia elineata* ass. prov.
    - 1214 Habitats of the western Gariiep mountains; 100 - 200 m, south-west facing slopes
      - Association: *Acrotome pallescens* - *Astridia alba* ass. prov.
  - 122 Leeward habitats of the escarpment ranges; 450 - 950 m
    - Alliance: *Chrysocoma puberula* - *Menodora juncea* all. prov.
    - 1221 Slope habitats, south facing
      - Association: *Cheilanthes capensis* - *Zygophyllum leptopetalum* ass. prov.
    - 1222 Slope habitats, west facing
      - Association: *Ruschia brevibracteata* - *Lycium hirsutum* ass. prov.
    - 1223 Slope habitats, north-east facing
      - Association: *Tripteris polycephala* - *Crotalaria meyeriana* ass. prov.
- 2 Habitats of the Nama Karoo
  - Order: *Sarcocaulon crassaule* - *Blepharis furcata* ord. prov.
  - 22 Slope habitats of the Nama Karoo within the mountain area
    - Sub-order: *Kleinia longiflora* - *Hermannia stricta* sub-ord. prov.
    - 221 Habitats of the Gariiep region and leeward of the escarpment ranges
      - Alliance: *Ceraria namaquensis* - *Aloe dichotoma* all. prov.
      - 2211 Favourite habitats in rock shelters
        - Association: *Pachypodium namaquanum* ass. prov.

- 2212 Habitats of the western Gariep mountains; 100 - 200 m, north-east facing slopes  
Association: *Zygophyllum microcarpum* ass. prov.
- 2213 Habitats of the eastern Gariep mountains; 50 - 300 m, south-west facing slopes  
Association: *Brownanthus nucifer* - *Ruschia abbreviata* ass. prov.
- 2214 Habitats of the eastern Gariep mountains; 200 - 700 m, mostly north-east facing slopes  
Association: *Euphorbia decussata* ass. prov.
- 22141 Dry habitats without high altitude species  
Typicum: *Euphorbia decussata* typ. nov.
- 22142 Favourite habitats on higher altitude, 400 - 700 m  
Sub-association: *Ruschia spinosa* sub-ass. prov.
- 2215 Habitats of the eastern Gariep mountains close to the Orange valley;  
Elevation 50 - 500 m, mostly north-east facing slopes  
Association: *Euphorbia virosa* - *Euphorbia gariepina* ass. prov.
- 21 Habitats on gravelly flood plains and drainage lines  
Sub-order: *Codon royenii* - *Trichodesma africanum* sub-ord. prov.
- 211 Habitats on gravelly flood plains and drainage lines within the Nama Karoo  
Alliance: *Calicorema capitata* - *Wellstedtia dinteri* all. prov.
- 2111 Habitats on footslopes leeward of the escarpment ranges  
Association: *Euphorbia mauritanica*\_Gariep - *Zygophyllum decumbens* ass. prov.
- 2112 Habitats on footslopes of the eastern Gariep mountains, 200 - 450 m  
Association: *Calicorema squarrosa* ass. prov.
- 2113 Habitats on footslopes of the eastern Gariep mountains, 100 - 200 (300) m  
Association: *Adenolobus garipensis* ass. prov.
- 2114 Habitats on drainage lines of the eastern Gariep, 200 - 450 m  
Association: *Sisyndite spartea* - *Rogeria longiflora* ass. prov.
- 2115 Habitats on gravelly flood plains of the eastern Gariep mountains  
Association: *Prenia tetragona* - *Psilocaulon subnodosum* ass. prov.
- 212 Habitats on gravelly flood plains and drainage lines with additional species  
of the Succulent Karoo  
Alliance: *Stipagrostis namaquensis* all. prov.
- 2121 Habitats on elevation of 200 - 450 m  
Association: *Leucophrys mesocoma* - *Monechma mollissimum* ass. prov.
- 2122 Habitats on elevation of 450 - 550 m  
Association: *Monechma spartioides* - *Cadaba aphylla* ass. prov.
- 1131 Habitats on the Orange River terraces  
Association: *Brownanthus pubescens* ass. prov.
- 3111 Species of the gallery forest along the Orange River banks  
Community: *Rhus pendulina* - *Ziziphus mucronata* com.
- 3211 Species of edaphically salt habitats on ravines  
Community: *Tamarix usneoides* - *Cyperus marginatus* com.
- 3212 Open sand plains  
Community: *Stipagrostis obtusa* com.
- 3 Special habitats (Pioneers, Ruderals, Phreatophytes)

### *Description of the vegetation units*

The vegetation of the Richtersveld is distinguished into five different units according to floristic and ecological criteria. The western part of the Richtersveld is covered with a dwarf shrub-land formation of mainly leaf succulent chamaephytes, which belongs to the Succulent Karoo. This includes the vegetation of the Sandveld, the Vandersterrberg - Stink-

fonteinberge, the Goariëp mountains and the silty plains (vlakte). The vegetation of the north-eastern Richtersveld shows a transition to a more scrubland formation of the Nama Karoo. Ultimately the hot eastern Gariep presents typical elements of the dry inland desert or semi-desert regions east of the Succulent Karoo such as *Euphorbia virosa* and *Euphorbia gariepina* (Jürgens 1991). The vegetation of the eastern Gariep includes the eastern Gariep mountains with Kouams mountains, De Hoop mountains, Maerpoort mountains, Rooiberg, Tatasberg, Gannakouriep region and the Rosintjebos mountains, the gravelly plains and drainage lines. The gallery forest of the Orange River valley is recognised as azonal vegetation and is therefore not included in the classification but introduced briefly.

The following sections describe the main units with their different communities. An ecological assessment complements the description. Details of life form distribution, mean ground cover, mean number of species and constancy, soil properties and habitat information can be taken from Fig. 3.8, Tab. 3.1-4 and Tab. A. T2-7 in the Appendix.

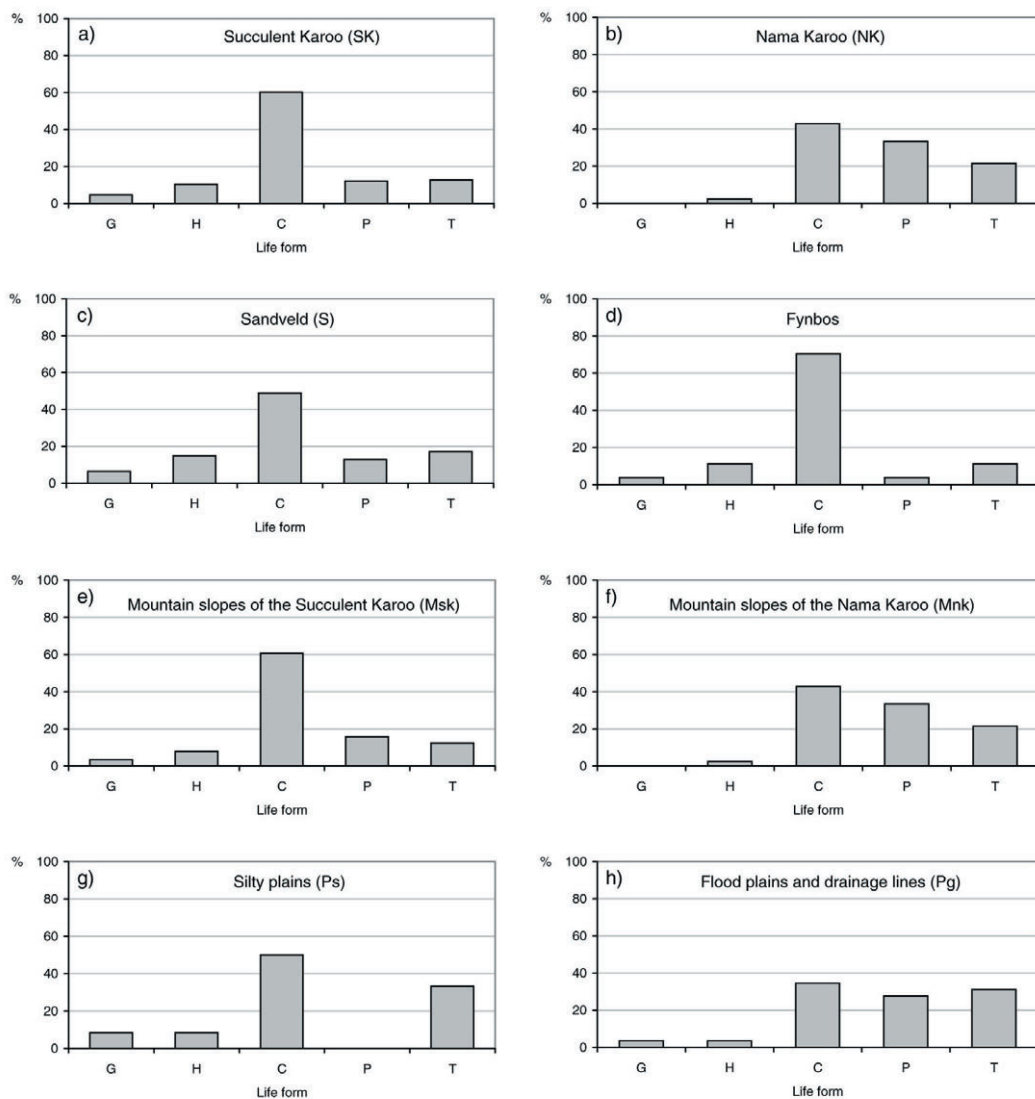


Fig. 3.8: Life form spectra of the main landscape units and the extrazonal Fynbos element (d).

Tab. 3.1: Relevé information for the syntaxa of the northern Richtersveld: minimum and maximum altitude (ALT min, max) in [m], exposition (EXP), minimum and maximum inclination (INCL min, max) in [%] and the geological unit (GEO, see chapter 2).

Code	Association	ALT		EXP	INCL		Geo
		Min	Max		Min	Max	
1111	Zygophyllum clavatum - Euphorbia brachiata	10	180			5	Q
1112	Zygophyllum morgsana - Hermannia trifurca	120	450			16	Q
11211	Cheiridopsis robusta - Ruschia leucosperma	150	600			(3) 40	Q
11212	Aridaria noctiflora s. noctiflora - Trachyandra muricata						
12111	Elytropappus rhinocerotis - Merxmuellera dura	1200		W			SEQ
12112	Pteronia divaricata - Berkheya canescens	1120	1200	W			SEQ
1212	Antizoma miersiana - Ruschia Tumidula_black fruits	540	830	W	12	55	AG3
1213	Crassula grisea - Ruschia elineata	460	950	SW	2	84	AG1
1214	Acrotome pallescens - Astridia alba	150	260	SW	55	75	AG1
12211	Cheilanthes capensis - Zygophyllum leptopetalum	450	955	S	14	90	AG1, Kh2Gr, AG3
12212	Ruschia brevibracteata - Lycium hirsutum	440	620	W	36	36	AG1
12213	Tripteris polycephala - Crotalaria meyeriana	500	640	N	36	36	Kh2Gr, Kh1L
2211	Pachypodium namaquanum	80	790 (1000)	NE, W	35	70	AG1, Kh1Hy
2212	Zygophyllum microcarpum	10	360	NE, W	18	90	AG1
2213	Brownanthus nucifer - Ruschia abbreviata	60	320	SE	35	70	AG1, Kh2Sc
22141	Euphorbia decussata	222	679	N			AG1, Kh2Gr
22142	Ruschia spinosa	420	740	SE,W	1	70	AG1, Kh2Sc
2215	Euphorbia virosa - Euphorbia gariepina	50	485	N	30	85	Kh2Sc, AG1
2111	Euphorbia mauritanica Gariep - Zygophyllum decumbens	300	550		3	65	Kh2Sc, Kh1L, AG1
2112	Calicorema squarrosa	200	500		15	90	Kh2Sc, Kh1L, AG1
2113	Adenolobus garipensis	121	348				AG1, Kh2Gr
2114	Sisyndite spartea - Rogeria longiflora	121	540			5	Q
2115	Prenia tetragonia - Psilocaulon subnodosum	300	620	S	2	7	Q
	Stipagrostis obtusa flood plain						
2121	Leucophris mesocoma - Monechma mollissimum	170	440	NE		3	Q
2122	Monechma spartioides - Cadaba aphylla	470	540	SE	2	9	Q
1131	Brownanthus pubescens	110.0	250.0				Q
3211	Tamarix usneoides - Cyperis marginatus	121	348				Q
3111	Rhus pendulina - Ziziphus mucronata						

Tab. 3.2: Floristic and plant structural information for the syntaxa of the northern Richtersveld: number of relevés (PNR), mean species number (SPEC No), mean ground cover (COV) in [%] and the life form spectra in [%]. H = hemicryptophytes; G = geophytes; P = phanerophytes; C = chamaephytes and T = therophytes. The last two columns show the growth form leaf succulent (l su) and stem succulent (s su) in [%].

Code	Association	PNR	SPEC No	COV	G	H	C	P	T	l su	s su
		n	n	%	%	%	%	%	%	%	%
1111	Zygophyllum clavatum - Euphorbia brachiata	10	20	16	6.4	14.9	48.9	12.8	17.0		
1112	Zygophyllum morgsana - Hermannia trifurca	20	14 (23)	28 (50)							
		mean	17	22							
11211	Cheiridopsis robusta - Ruschia leucosperma	16	9 (25)	16 (40)	8.3	8.3	50	0	33.3		
11212	Aridaria noctiflora s. noctiflora - Trachyandra muricata	9	8 (15)	17 (40)							
		mean	9	17							
12111	Elytropappus rhinocerotis - Merxmuellera dura	3	27	53	3.7	11.1	70.4	3.7	11.1	44.0	16.0
12112	Pteronia divaricata - Berkheya canescens	3	27	47							
1212	Antizoma miersiana - Ruschia Tumidula_black fruits	6	15	49							
1213	Crassula grisea - Ruschia elineata	10	27 (44)	23							
1214	Acrotome pallescens - Astridia alba	5	14	3	3.4	7.9	60.7	15.7	12.4		
12211	Cheilanthes capensis - Zygophyllum leptopetalum	12	18	28							
12212	Ruschia brevibracteata - Lycium hirsutum	5	16	14							
12213	Tripteris polycephala - Crotalaria meyeriana	10	23	14							
		mean	18	26							
2211	Pachypodium namaquanum	10	7	11							
2212	Zygophyllum microcarpum	10	7	2							
2213	Brownanthus nucifer - Ruschia abbreviata	10	8	8	0.0	0.0	50.0	36.4	13.6		
22141	Euphorbia decussata	10	4	8							
22142	Ruschia spinosa	8	8	10							
2215	Euphorbia virosa - Euphorbia gariepina	10	3	3							
2111	Euphorbia mauritanica Gariep - Zygophyllum decumbens	7	9	6						35.0	28.0
2112	Calicorema squarrosa	8	4	5							
2113	Adenolobus garipensis	5	2	6							
2114	Sisyndite spartea - Rogeria longiflora	12	6	3	2.9	5.7	34.3	28.6	28.6		
2115	Prenia tetragonia - Psilocaulon subnodosum	10	10	10							
	Stipagrostis obtusa flood plain										
2121	Leucophris mesocoma - Monechma mollissimum	10	6	10							
2122	Monechma spartioides - Cadaba aphylla	9	15	17							
		mean	7	8							
1131	Brownanthus pubescens	4	3	15	0.0	0.0	99.0	0.0	0.0		
3211	Tamarix usneoides - Cyperis marginatus	4	3	13							
3111	Rhus pendulina - Ziziphus mucronata				0.0	0.0	0.0	99.0	0.0		



## 1 Habitats of the Succulent Karoo

Order: *Tetragonia fruticosa* - *Pteronia glabrata* ord. prov.

Diagnostic species: *Tetragonia fruticosa*, *Pteronia glabrata*, *Asparagus capensis*, *Euphorbia ephedroides*, *Othonna furcata*, *Tetragonia echinata*, *Othonna cylindrica*, *Hermannia cuneifolia*, *Pteronia ciliata*, *Stoeberia beetzii* and *Zygophyllum cordifolium*

General aspect: This order is formed by mainly leaf succulent chamaephytes of the characteristic dwarf shrub-land formation. The vegetation of the Sandveld habitats and the western part of the mountain region with the Vandersterrberg - Stinkfonteinberge are joined together under this order. See the results of the synoptic table A. T7.

Topography: Surface relief ranges from low sandy plains at the coast to steep slopes of the high escarpment. In addition the footslopes of the escarpment and the inner-mountain basins have mostly a constant downwards slope with an average value of 2 - 3 %.

Climatic aspects: The maximum precipitation occurs in winter, when moderate air temperatures presuppose lower evapo-transpiration values. The air humidity is moderate due to the frequently penetrating fog coming in from the Atlantic Ocean.

Vegetation pattern and cover: The vegetation along the coastal plain forms a dense regular pattern with rare interruptions by undulating dunes, where the dune crests show a more open vegetation cover with the dwarf shrubs overtopped by certain phanerophytes. These plants, e.g. *Stoeberia utilis* are able to collect a surplus of water from the fog, visible by dark wet spots directly under the plant. The vegetation of the steep escarpment slopes shows a dense but irregular pattern produced by the irregular occurrence of rock boulders and rock faces. This is mainly true for the granite Goariep mountains. Where narrow ravines or groups of boulders or large bedrock outcrops occur, the dwarf shrub is mainly replaced by phanerophytes, which profit from the benefit of ground water. As mentioned previously the majority of the Succulent Karoo species are chamaephytes (60 %), 12 % are phanerophytes and 13 % are therophytes. Hemicryptophytes (10 %) and geophytes (5 %) are also represented. From these life forms 45 % are leaf succulent and 15 % stem succulent (Fig. 3.7). The ground cover is comparatively dense with a mean value of 26 %. The highest density for the Richtersveld is reached on the rain facing escarpment slopes with up to 53 % (Tab. 3.2).

Floristic composition: Several taxa such as the genera *Tylecodon*, *Crassula*, *Zygophyllum*, *Tetragonia*, *Galenia*, *Euphorbia*, *Pelargonium*, *Sarcocaulon* and the family Asclepiadaceae are restricted to the Succulent Karoo. Additionally most genera of the Mesembryanthemaceae are limited to this floristic region representing its largest family. In one degree square 27 genera dominate the central parts of the Succulent Karoo (Jürgens 1991). The mean number of species is 8 - 27 per 100 m<sup>2</sup> and reaches 44 at Numees, a centre of high diversity (Tab. 3.2). Even though the habitats of the low coastal plain and the seaward high escarpment ranges differ in substratum, some species occurs on both. *Stoeberia beetzii*, *Othonna cylindrica* and *Tetragonia fruticosa* for example, all leaf succulent chamaephytes, colonise mainly the sand habitats throughout the Namaqualand Sandveld. Nevertheless they are companions in the communities of the Vandersterrberg - Stinkfonteinberge and the Koeroegab mountains on west- and south facing slopes (see description below). Not only do the dominating leaf succulent chamaephytes give the Succulent Karoo its typical character but also the widespread stem succulents of the genus *Euphorbia*. For example

*Euphorbia ephedroides* and *Euphorbia chersina* occur on sandy sites on the coastal plain as well as on the fine-grained soil pockets of rain facing steep slopes throughout the Richtersveld Mountain District. The two *Euphorbia*-species mentioned are linked to the Southern Namib District, where their distribution area is extended. The drought-deciduous *Euphorbia mauritanica* is very variable and ranges from a dwarf (approx. 16 cm high) variety *corallothamnus* near Alexander Bay, to a 130 cm high variety *mauritanica* distributed throughout the Sandveld. The common form of the Richtersveld Mountain District is called *foetens* (Williamson 2000). Another spectacular phenomenon characterises the western Richtersveld and the whole Namaqualand: after the winter rains millions of flowers cover the surface as far as the horizon. Numerous chamaephytes of the genera e.g. *Ruschia*, *Drosanthemum* and *Lampranthus* (Mesembryanthemaceae) with their pink flowers join the mostly yellow flowering chamaephytes of the genera *Pteronia*, *Othonna* and *Euryops* (Asteraceae). The therophytes *Dimorphotheca*, *Heliophila*, *Osteospermum*, *Didelta* and others complete the colourful palette with white, blue and orange.

## 1.1 Habitats on the plains and basins of the Succulent Karoo

Sub-order: no diagnostic species

Diagnostic species: see text.

Lacking its own differential species group, this sub-order combines the plains of the Succulent Karoo characterised by the absence of the diagnostic species group of the 'Tylecodon paniculatus - *Osteospermum armatum* sub-ord.' of the western mountain region.

### 1.1.1 Sandy habitats of the coastal plain (Sandveld)

Alliance: *Eberlanzia ebracteata*\_coast - *Lebeckia multiflora* all. prov.

Diagnostic species: *Lebeckia multiflora*, *Eberlanzia ebracteata*\_coast, *Euphorbia mauritanica* v. *mauritanica*, *Cladoraphis cyperoides*, *Ehrharta brevifolia* v. *cuspidata*, *Salsola tuberculata* and *Karrochloa schismoides*

General aspect: The comparatively dense dwarf shrub-land has a monotonous appearance when looking from the escarpment to the Atlantic Ocean. Only the red sand dune and the firm sand ridge, that forms longitudinal bands nearly parallel to the coastline, interrupt it. Peaks such as the Grootberg and Springklipberg are rare rock outcrops on the sandy plain. The differentiated table A. T2. and the synoptic table A. T7. gave the basis for the following subdivision. The sandy habitats alternate with the more silty habitats along the coastal plain. Despite the local vicinity of both, they differ in their vegetation physiognomy and composition. Therefore the latter is described under the alliance 'Silty habitats of the coastal plain (Sandveld) and the inner-mountain basins' (1 1211 = code of classification), where they are related.

Topography: The part of the Sandveld studied in this work is situated along the coast, where it occupies an elongated tract of less than 50 km wide from the Oragne River valley to the Holgatrivier. The altitudinal range differs from 10 m near the Atlantic Ocean to 450 m at the foot of the escarpment. The surface is undulating where sand accumulated to form longitudinal north-south aligned dunes.

Geology: At the beginning of the Tertiary the sand was deposited at the coastline. The origin of the sand is to be found in the mountain region, where the sand was removed from the

surface of the extended plains, such as the Springbokvlakte, under arid conditions and was transported to the coastal plain (Villiers and Söhnge 1959).

**Soils:** The white sand on the coastline is succeeded further inland by the red sands. An increasing iron coating on the quartz particle causes the red colour which is evident from the coast to the inland and which is prevented by the sea salt near to the coast. The soils have high basic portions and depths of more than 30 cm. The universal presence of crusts, mainly consisting of lime and gypsum ( $\text{CaSO}_4$ ), is remarkable for coastal plain habitats. In some places soda ( $\text{Na}_2\text{CO}_3$ ) and NaCl reach high values and  $\text{MgSO}_4$  is frequently present. In arid and semi-arid regions the input of the readily soluble salt is affected by aerosols from the sea (Scheffer & Schachtschabel 1989). The soils have no stone content until the crusts. Most of the sites provide a deep sand body with only 0.5 % vol. clay, 1.1 % vol. silt and 89 % vol. medium sand. The crust begins on average at a depth of 70 cm (Tab. 3.3 and 3.4).

**Climatic aspects:** The oceanic influence on the plant formation is very strong; air humidity is higher and daily temperature amplitude lower than further inland and the annual temperature is moderate (see chapter 1.2.4), increasing from the coast to the footslopes of the escarpment. The precipitation is low with c. 50 mm.

**Vegetation pattern and cover:** In contrast to the shallow soils of the silty habitats (see ass. 1121), the deep sand body allows a higher growing formation, which have a height of 80 to 200 cm (syntaxa code: 1111 and 1112). The relatively high mean ground cover, about 22 %, is only surpassed by the vegetation density on the escarpment habitats (Tab. 3.2). The dwarf shrub formation is made up of mainly leaf succulent chamaephytes (49 %) and leaf succulent phanerophytes (13 %). Hemicryptophytic grasses (15 %) and geophytes (6 %) are frequently companions (Tab. 3.2, Fig 3.8.c).

**Floristic composition:** The differential species *Othonna cylindrica* (l su), *Eberlanzia ebracteata*\_coast (MCh l su), *Salsola tuberculata* (MCh l su), *Lebeckia multiflora* (NP) and *Cladoraphis cyperoides* (H) give this formation its typical appearance. Herewith *Othonna cylindrica* and *Eberlanzia ebracteata*\_coast dominate the formation. Typical therophytes are *Arctotis fastuosa*, *Arctotis auriculata* and *Zaluzianskya affinis*. The mean number of species with 17 per 100 m<sup>2</sup> is moderate and reaches 23 species in some places (Tab. 3.2).

### 1111 Habitats at the coastline on white sands

Association: *Zygophyllum clavatum* - *Euphorbia brachiata* ass. prov.

**Diagnostic species:** *Zygophyllum clavatum*, *Euphorbia brachiata*, *Zygophyllum cordifolium*, *Hermannia cuneifolia*, *Pteronia glabrata*, *Sarcocaulon patersonii* and *Dregeochloa pumila*

**General aspect:** Habitats bordering directly on the coastline provide different environmental conditions than the habitats further inland, which are shown in a different vegetation composition.

**Topography:** The coastline consists of white, firm and loose, sand and borders directly on the Atlantic Ocean. The loose sand forms longitudinal north-south aligned dunes. The dune crests reach no more than 1 - 2 m in height and 5 - 10 m in diameter.



Geology: The firm sand was developed *in situ* under weathering conditions during the early Tertiary. The loose wind-blown sand was deposited during arid conditions and originates from the extended plains of the mountain region (Villiers and Söhnge 1959).

Soils: The '*Zygophyllum clavatum* - *Euphorbia brachiata* ass.' colonises white medium sands where a mixture of lime and gypsum crust lies at a depth of 50 - 60 cm (Tab. 3.3). The conductivity near the crust is high (39,8 - 3162,3 mS/cm, Tab. 3.4). The carbonate content reaches 2,5 - 10 % wt. (Tab. 3.4) and also soda and NaCl have high values. The colour of wet sand presents a grey to pale brown indicating CaCO<sub>3</sub> (calcite) and CaSO<sub>4</sub> (gypsum) and a low content of iron oxides (Munsell 1994) in contrast to the sand ten kilometre further inland. The primary root system reaches down to a depth of 55 cm within the pale brown sand, which is banded by humus substances.

Climatic aspects: The coastal habitats are influenced by the lowest air temperature (17°C) and the highest air humidity of the Richtersveld but on the other hand they receive the lowest amount of precipitation, c. 10 - 50 mm p. a. (chapter 1.2.4). The low precipitation values are more or less offset by the frequent incidence of fog. It is important to mention the fact that the species occurring directly in the vicinity of the Atlantic Ocean have to cope with the salty sea spray (air and ground).

Vegetation pattern and cover: The vegetation close to the coast, on firmer sand, reaches heights of 30 - 40 cm (A. P3). Further inland, where the sand extends to over 65 cm above the crust, the vegetation can reach up to a height of 1.5 m. This vegetation cover is looser and the individuals have a better constitution than the surrounding vegetation. These two types also alternate within the loose sand where the former colonises the inter-dune sections and the latter the dune crests. The two types are described in the following section as two different sub-associations.

Floristic composition: The leaf succulent chamaephytes *Zygophyllum clavatum*, *Hermannia cuneifolia* (MCh) together with *Pteronia glabrata* (MCh l su) and *Othonna furcata* (NP s + l su) give the association its typical appearance.

Distribution: The occurrence of *Zygophyllum clavatum*, *Sarcocaulon patersonii* (NCh s su) and *Dregeochloa pumila* (H) is unique to the Richtersveld. Their distribution centre lies on the coastal plain of Namibia in the floristic district of the southern Namib (Succulent Karoo Region) and reaches their southern border 10 - 20 km further south of Alexander Bay.

#### 11111 Firm sand habitats without psammophytes

Typicum: *Zygophyllum clavatum* - *Euphorbia brachiata* typ. nov.

Plots: 5986, 6030 10250, 10254, 10256

Diagnostic species: see text

The main feature of the firm sand habitats is the lack of species that appear on deep sand bodies (psammophytes). Along the coastline firm sand habitats occur and alternate further inland with small longitudinal sand dunes in a north-southern alignment. The psammophytes are described in the following section. The firm white sand lies over a gypsum crust at a depth of 20 - 30 cm. The air temperature and air humidity are moderate. The sea spray influences the habitats.

### 1112 Habitats on consolidated sand body with psammophytes

Sub-association: *Othonna sedifolia* - *Tripteris oppositifolia* sub-ass. prov.

Plots: 10249, 10251, 10252, 10253 and 10255

Diagnostic species: *Othonna sedifolia*, *Ruschia Tumidula\_black* fruits creeping, *Jamesbrittenia* 110558, *Tripteris oppositifolia*, *Trachyandra falcata* and *Pelargonium ceratophyllum*

Psammophytes of the white sand are combined with psammophytic species, which occur throughout the Sandveld, where a deep sand body occurs. The habitats are situated on the sand plain or on dune crests where the deep sand body extends to 65 cm above the gypsum crust.

*Othonna sedifolia* (MCh I + s su), *Ruschia Tumidula\_black* fruits creeping (MCh I su) and *Lycium cinereum* (MCh frut) assemble with *Tripteris oppositifolia* (MCh I su), *Trachyandra furcata* (T I su) and the rare *Pelargonium ceratophyllum* (MCh I + s su). The latter species are also common on deep red sand bodies at a distance of 10 km from the coast further east (described below).

*Othonna sedifolia*, *Lycium cinereum*, *Tripteris oppositifolia* and *Trachyandra furcata* also occur in the mountain region of the Richtersveld along drainage lines or in rocky shelters and can therefore be interpreted as indicators for favourable conditions in the sense of high water storage. *Tripteris oppositifolia* is common in the whole Namaqualand Sandveld District and also occurs in the Cape Floristic Region.

### 1112 Habitats of the inner-coastal plain on red sands

Association: *Zygophyllum morgsana* - *Hermannia trifurca* ass. prov.

Diagnostic species: *Zygophyllum morgsana*, *Hermannia trifurca*, *Galenia collina*, *Lebeckia cinerea* and *Stipagrostis dregeana*

General aspect: The second important association of the sandy habitats is developed 10 km from the coast and extending to the red dune.

Topography: The inner-coastal plain is undulating with a slight change from dunes and inter-dunes north-south aligned. Only the red dune reaches high, isolated between the silty sand ridge and the Goariepvlaakte further inland. Near the silty sand ridge the sand and silty sand habitats form a patchy pattern in the transition zone.

Geology: The loose sand was transported from the sandy plains of the mountain region to the coast by wind action. Today the vegetation cover fixes most of the sand. It is of terrestrial origin in contrast to the younger marine white sands at the coast (Villiers & Söhnge 1959).

Soils: The habitats are comparable with those near the coastline in the case of depth, grain size and absent horizons. Only the content of soda and gypsum is low and there are only slight traces of NaCl (A. 13) The red sand obtains its colour from an increasing iron coating around the sand particle. Gypsum and lime crusts are consolidated in the ground.

Vegetation pattern and cover: The '*Zygophyllum morgsana* - *Hermannia trifurca* ass.' (A. P4) forms a patchwork with the '*Cheiridopsis robusta* - *Ruschia leucosperma* ass.' at the transition to the firm sand ridge. This means an alternation of high (up to 2 m) and low (up to 50 cm) vegetation. The mean ground cover is, with 28 %, higher than the former with only 16 % (Tab. 3.2).

Floristic composition: *Zygophyllum morgsana* (NP I su), *Galenia collina* (MCh I su) and *Galenia namaensis* (MCh I su) are the main leaf succulent shrubs. The non-succulent differential species *Lebeckia cinerea* (NP) and *Hermannia trifurca* (MCh), such as *Hermannia cuneifolia*

(Ch), are protected against the high insolation by minute grey hairs. *Zygophyllum morgsana* und *Lebeckia cinerea* are the most constant species of this association. *Stipagrostis ciliata* is a common grass in the Richtersveld but here on the inner-coastal plain it occurs with a high constancy. The mean species number reaches 14 per 100 m<sup>2</sup> (Tab. 3.2).

#### 11121 Habitats on red sands

Sub-association: *Jordaaniella clavifolia* - *Chaetobromus involucratus* s.-ass. prov.

Diagnostic species: *Chaetobromus involucratus* and *Jordaaniella clavifolia*

The leaf succulent and creeping *Jordaaniella clavifolia* forms extended clusters on the ground of 1 - 5 m in diameter, and so it prevents higher growing succulents to germinate or grow between its creeping shoots. Only smaller species, such as *Chaetobromus involucratus* (H) or *Galenia mezziana* (H) and many therophytes, are able to grow among these succulents. There is a second leaf succulent creeper, which shares the same habitat. *Jordaaniella cuprea* has larger leaves but its shape is very similar to the latter. It forms one of the two variants of this sub-association. The dense vegetation cover with tall species such as *Euphorbia mauritanica* v. *mauritanica*, *Zygophyllum morgsana*, *Lebeckia multiflora* and *Lebeckia cinerea* is interrupted by this group. In this way a patchy pattern is developed on the red sand habitats.

The wet sand shows a brown to dark brown colour, which provides the information, that the iron oxide goethite content is high (Munsell 1994). There is no carbonate throughout the whole profile except near the calcrete at a depth of 70 to 90 cm (Tab. 3.3).

Two variants of this sub-association developed on the undulating sand plain due to the presence of dune crests and inter-dune valleys.

#### 111211 Habitats on sandy sheets and inter-dune sections

Variant: *Jordaaniella cuprea* - *Crassula atropurpurea* v. *cultriformis* var. prov.

Plots: 5926, 5962, 5965, 5966, 5967, 5969, 5970, 5971 and 5972

On sand sheets or in dune valleys *Jordaaniella cuprea* (MiCh I su), *Crassula atropurpurea* v. *cultriformis* (NCh I su) and *Monechma incanum* (Ch) are typical companions.

#### 111212 Habitats on dune crests

Variant: *Stoeberia utilis* - *Ruschia Sarmetosa\_ascending* fruits var. prov.

Plots: 5964, 5973, 6052, 10263, 10264 and 10265

The high growing *Stoeberia utilis* (NP I su) occurs on the dune crests, which is able to gather water from fog with its long shoots. *Ruschia Sarmetosa\_ascending* fruits (MCh I su) and *Galenia namaensis* (MCh) joins the dominating phanerophyte.

#### 11122 Habitats on the red dune

Sub-association: *Cladoraphis spinosa* - *Limeum fenestratum* v. *fenestratum* sub.-ass. prov.

Plots: 5981, 10270, 10271, 10272, 10273, 10274 and 10275

Diagnostic species: *Cladoraphis spinosa*, *Limeum fenestratum* v. *fenestratum*, *Coelanthum grandiflorum*, *Wahlenbergia prostrata*, *Conicosia elongata* and *Limeum aethiopicum*

General aspect: The red dune is a conspicuous object within the monotonous landscape of the Sandveld. The shining red sand accumulated in the shelter of the rock outcrops Springklipberg and Grootberg and borders the Goariepvlakte in front of the escarpment.

Topography: The topographical shape of the red dune forms an almost longitudinal aligned inter-rogation mark with a length of 55 km and a height of 70 m from the base to the crest.

Geology: The terrestrial red sand possibly belongs to the period of Tertiary aridity typified by the red Kalahari sand. The origin is thought to be in areas of deflation within the mountain region such as the Springbokvlakte (Villiers & Söhnge 1959).

Soils: On account of the deep sand body the influence of any crust is only to be expected at the edge of the sand dune. The conductivity is low (20  $\mu\text{S}/\text{cm}$ ); the content of salt is poor, only a low content of soda,  $\text{NaSO}_4$  and potassium is to be expected (A. T13). The deep sand body provides a very good water storage which leads to favourable growth conditions despite a low content of nutrients such as nitrate and phosphate.

Vegetation pattern and cover: The vegetation cover is dominated by one nano-phanerophyte and hemicyptophytic grasses, therefore the appearance is remarkable within the usual dwarf shrub formation of the Sandveld. The mean ground cover is 24 % (Tab. 3.2).

Floristic composition: This sub-association with *Wahlenbergia prostrata* and *Limeum aethiopicum* is characterised by a high cover of *Lebeckia cinerea* (NP), both *Cladoraphis*-species *spinosa* (H) and *cyperoides* (H) and *Stipagrostis ciliata* (H). The mean species number amounts to 17 (Tab. 3.2).

Distribution: *Lebeckia cinerea* and *Limeum fenestratum* (T/H) can be interpreted as a link to the large dune field of the Central Namib between Lüderitz and Walfishbay. *Limeum aethiopicum* (T/H) is widespread with its centre in the Eastern Karoo Domain of the Nama Karoo Region.

### 11123 Sandy habitats in the zone of high corrasion south of the lower Orange River

Sub-association: *Brownanthus arenosus* sub-ass. prov.

Plots: 6021, 6026, 6038, 6039, 6040, 6041, 6042, 6043, 6070 and 10081

Diagnostic species: *Brownanthus arenosus* and *Aridaria noctiflora* v. *noctiflora*

Above all the '*Brownanthus arenosus* sub-ass.' (MCh s + l su) occurs in the seaward valley of the red dune where it is connected to the zone of high corrasion in the north. This sub-association has the lowest mean number of species (8) within the Sandveld and a mean ground cover of 17 % (Tab. 3.2). Its community structure resembles the '*Brownanthus pseudoschlichtianus* - *Drosanthemum inornatum*' community on silty sands; both share some companions e.g. *Aridaria noctiflora* s. *noctiflora*.

### 112 Silty habitats of the coastal plain (Sandveld) and the inner-mountain basins

Alliance: *Brownanthus pseudoschlichtianus* - *Drosanthemum inornatum* all. prov.

Diagnostic species: *Brownanthus pseudoschlichtianus*, *Drosanthemum inornatum*, *Lampranthus otzenianus* and *Eberlanzia ebracteata\_inland*.

General aspect: The dwarf shrub formation on level silty sand habitats is part of a zonal vegetation type of the Succulent Karoo (Jürgens 1991). It occurs along the coastline on both sides

of the Orange River, in the Namaqualand Sandveld District, in the southern Namib and in the Richtersveld Mountain District. Within the different floral districts (Namaqualand Sandveld District and Western Richtersveld Mountain District) silty sand habitats appear on the coastal plain, where it forms a mixture with the pure sand habitats, and in the centre of the Richtersveld mountains on inner-mountain basins and along drainage lines in sheltered positions. Hence the climatic conditions differ near the coast and within the centre of the Richtersveld mountains, the floristic composition is very similar. See the results of the differentiated table A. T3 and the synoptic table A. T7.

**Geology:** The silty sands are part of rock waste, which choked the valleys and plains during an arid period of the early Tertiary. Due to the dry conditions the sand was transported from the inner-mountain basins of the mountain region to the coastal plain. The inner-mountain basins near to the escarpment range were protected against the wind by a vegetation cover, so that the silty sand was fixed. Under weathering conditions the sand was transformed further and a lime crust developed.

**Soils:** The grain composition of these habitats is marked by a high silt content (33 - 44 %) compared to the sand habitats with only 1 %. The stone content varies from 4 to 8 %. The mainly lime crust lies nearer to the surface, 20 - 50 cm, than under the sand habitats, 50 - 90 cm (Tab. 3.3). The salt content and nutrients are low, apart from near the crust where the conductivity increases and the  $\text{CaCO}_3$  content is remarkably high: 5 - 25 % wt. (Tab. 3.4).

**Vegetation pattern and cover:** The vegetation of the silty habitats, where the crust lies nearer to the surface than under the sand habitats, develops a lower cover with a height of up to 50 cm in contrast to the vegetation of the sand habitats with up to 2 m. The mean ground cover varies between 16 - 17 % (Tab. 3.2). The majority of the life forms are chamaephytes (50 %), no phanerophytes, 8 % hemicryptophytes, 8 % geophytes and 33 % therophytes (Tab. 3.2, Fig. 3.8.g); 90 % of the chamaephytes are leaf succulent, 28 % are stem succulent.

**Floristic composition:** The dominating species *Brownanthus pseudoschlichtianus* (MCh I + s su) reaches a mean ground cover of 10 %. The other species such as *Drosanthemum inornatum* (MCh I su), *Lampranthus otzenianus* (MCh I su) and *Eberlanzia ebracteata\_inland* (MCh I su) occur frequently but with a lower constancy of 32 % compared to the former with a constancy of 96 %. The mean number of species is low and amount to only 8 - 9 (Tab. 3.2). *Eberlanzia ebracteata\_inland* prefers the habitats near the footslopes of the surrounding mountains, where the water supply is better than in the centre of the plain. Nevertheless, *Drosanthemum inornatum* occurs throughout the whole plain. *Lampranthus otzenianus*, a light pink flowering dwarf shrub has a more patchy appearance.

**Distribution:** The differential species *Drosanthemum inornatum*, *Lampranthus otzenianus* and *Eberlanzia ebracteata\_inland* have their main distribution centre such as *Brownanthus pseudoschlichtianus* along the coastline in the Succulent Karoo.

#### *Heuweltjies* or Mima-like mounds

A special feature are the *heuweltjies* or Mima-like mounds observed on the silty sand plains covered by the described community. These are circular calcrete mounds, 5 - 50 m in diameter and a height of 0.1 to 0.5 m (Villiers & Söhnge 1959, Milton et al. 1997). The occurrence of

these structures reaches densities of about 35 *heuweltjies* per km<sup>2</sup>. The Mima-like mounds are thought to be a product of animal activities (first termites, later ants and voles). They differ from their surroundings in soil properties and vegetation composition. Whereas the surrounding soil profiles show a clear subdivision in different layers this subdivision is absent along the profiles of the *heuweltjies*. The grain composition shifts from silty sand to sandy silt with 57 % silt. High pH-value (8,2) and a high CaCO<sub>3</sub> content throughout the whole profile (3 - 25 % wt.) are common attributes of these soils (Tab. 3.4).

The vegetation cover of the *heuweltjies* is with 2 to 5 % less dense than their surroundings (16 - 17 %). The surface patches lack perennials and are covered with ephemerals after the precipitation period in winter. Near the footslopes and on the firm sand ridge in the Sandveld it could be observed that *Eberlanzia cyathiformis* often colonises the *heuweltjies*.

Mima-like mounds occur throughout the whole southern Africa (Esler & Cowling 1998). But these structures have also been observed in Northern Minnesota (Ross et al. 1967), in California (Cox 1984, 1990) and in New Mexico (Andersen & Kay 1999).

### 1121 Silty habitats of the coastal plain

Association: *Cheiridopsis robusta* - *Ruschia leucosperma* ass. prov.

Plots: 5927, 5928, 5959, 5960, 5961, 5963, 5968, 5975, 5976, 5977, 5979, 5980, 5982, 5985, 6019, 6023, 6024, 6025, 6029, 6031, 6033, 6034, 6035, 6036, 6037, 6047, 6051, 6053, 6066, 6067, 6068, 6071, 6072, 6073, 6074, 6132, 6136, 6138, 6151, 6183, 6184, 6186, 6187, 6188, 6189, 6190, 6193, 6194, 6195, 6196, 6200, 6201, 6202, 6203, 6204, 6206, 6207, 6284, 10118, 10216, 10220, 10228, 10257, 10258, 10259, 10260, 10261, 10262, 10268 and 10277

Diagnostic species: *Ruschia leucosperma* and *Cheiridopsis robusta*

At a distance of 20 km from the coast on a ridge of silty sand stretches parallel to the coast, the firm sand ridge, and on the Goariepvlakte 'Ruschia leucosperma - Cheiridopsis robusta' ass. occurs in its purest form. Poor stands of this association re-occur in the inner-mountain basins near the footslopes and in sheltered positions along the drainage lines, where silty sand pockets were able to remain.

Climatic aspects: At a distance of 30 to 40 km from the coast, the mean sunshine duration and the mean air temperature is higher than directly at the coast and nearly similar to the habitats of the inner-mountain basins. The air humidity at the latter might be lower than at the firm sand ridge.

Vegetation pattern and cover: The 'Cheiridopsis robusta - Ruschia leucosperma ass.' (A. P5) forms a confined patchwork with the communities of the sandy habitats (111), which results in a patchy appearance of high (up to 2 m) and low (up to 50 cm) vegetation as previously mentioned. The mean ground cover measures 16 % to 28 % of the red sand habitats (Tab. 3.2).

Floristic composition: Due to the patchwork of the two communities on sand and silty sand habitats at the coast the floristic composition of the 'Cheiridopsis robusta - Ruschia leucosperma' ass. is supplemented with several companions of the communities on sand such as *Stoeberia beetzii*, *Othonna cylindrica*, *Asparagus capensis* and others. It is therefore richer than the association in the inner-mountain basins. The mean species number comes to 9 per 100 m<sup>2</sup> in contrast to 14 for the red sand communities (Tab. 3.2).

Distribution: *Cheiridopsis robusta* (MiCh I su) has a restricted distribution area from the Holgat River in the Sandveld to the Walfish Bay in the southern Namib with some occurrence in the Western Richtersveld Mountain District.

### 1122 Silty habitats of the inner-mountain basins

Association: *Aridaria noctiflora* s. *noctiflora* - *Trachyandra muricata* ass. prov.

Plots: 5941, 5942, 5943, 5944, 5945, 5946, 5954, 5955, 5956, 5957, 5958, 5974, 6007, 6010, 6069, 6197, 6198, 6199, 6205, 6250, 6252, 6253, 6268, 6269, 10090, 10100, 10101, 10120, 10130, 10131, 10133, 10148, 10149, 10153, 10154, 10156, 10158, 10159, 10160, 10164, 10165, 10167, 10169, 10172, 10173, 10174, 10179, 10180, 10181, 10183, 10185, 10187, 10189, 10192, 10195, 10200, 10205, 10212, 10234, 10235, 10238, 10239, 10240, 10267, 10276, 10290, 10299, 10391, 10392 and 10451

Diagnostic species: *Aridaria noctiflora* s. *noctiflora* and *Trachyandra muricata*

Topography: The extended silty plains are interrupted by complex drainage systems with small channels and with broad dry riverbeds at the end of the system, where the silty plains change to flood plains. The plains have a constant downwards slope with an inclination of 2 - 5°.

Soils: The soils of the inner-mountain basins contains a fraction more clay (2.2 to 1.0 %) and more silt (44 to 33 %) than the silty sands of the coastal plain, and the stone content is higher, 4 to 8 % (Tab. 3.3).

Climatic aspects: The sea mists episodically reach the silty plains, and the benefit of the winter rain coming from south-west over the high escarpment ranges is still high compared to the eastern Gariep region. The air humidity is lower than at the coast and the mean air temperature is moderate.

Vegetation pattern and cover: The only pattern that is observed in the constant vegetation cover is the spot-like occurrence of the Mima-like mounds as previously mentioned. The low mean ground cover of 17 % is similar to the vegetation cover of the silty sand habitats at the coast (Tab. 3.2).

Floristic composition: The differential species *Aridaria noctiflora* s. *noctiflora* (H) and *Trachyandra muricata* (G) show a regular pattern with *Brownanthus pseudoschlichtianus* and *Drosanthemum inornatum* (A. P11). *Stipagrostis obtusa* (H), *Trachyandra bulbinifolia* (G), *Albuca spiralis* (G) and other geophytes are frequent companions. The low mean ground cover allows a diverse ephemeral meadow in winter that consists of the dominating *Oncosiphon piluliferum* (T), *Leysera tenella* (T), *Lotononis falcata* (T) and *Senecio piptocoma* (T). Near the footslopes the ground cover can reach 40 % where the number of species also increases from 8 (mean number of species) to 15 per 100 m<sup>2</sup> (Tab. 3.2). The inner-mountain basins are seasonally used as pastures in winter. Hence several indicators for disturbance or grazing are frequently companions, such as *Psilocaulon salicornioides* (MCh s + I su), *Mesembryanthemum squamulosum* (T I su), *Opophytum aquosum* (T I su) and others. The appearance of *Cheiridopsis robusta* (MiCh I su), *Ruschia leucosperma* (MCh I su) and *Eberlanzia ebracteata* (MCh I su) indicates a higher amount of sand because of their distribution centre on the sandy habitats at the coast. The silty soil pockets along the drainage lines might also be sandier because of the dominance of the previously named sand indicators.

Actual erosion risk to the plain surface

The investigation of the present erosion risk to the plain surface leads to the suggestion that the erosion processes today are higher than the accumulation processes. The figure 3.9 shows the contrast of 39 % phytogenic mounds to only 1 % down axis by sediment. In this context the amount of soil crusts is important. The amount of microbiotic crusts on the soil surface is with 20 % low in contrast to the physical crust with 70 %. Of note is the distribution of the crusts along the slope down to the plain (Fig. 3.10). The physical crust reaches the highest values on the footslope (88 %) and at the lower end of the plain with 100 %. While the highest amount of microbiotic crusts (56 %) is reached on the upper plain, where the physical crust shows the lowest amount with 44 %. Microbiotic crusts are restricted to the upper parts of the plain. The correlation between the amount of phytogenic mounds and microbiotic crusts is obvious. The lowest amount of phytogenic mounds (25 %) and therefore the lowest value of erosion were found where microbiotic crusts mainly cover the surface.

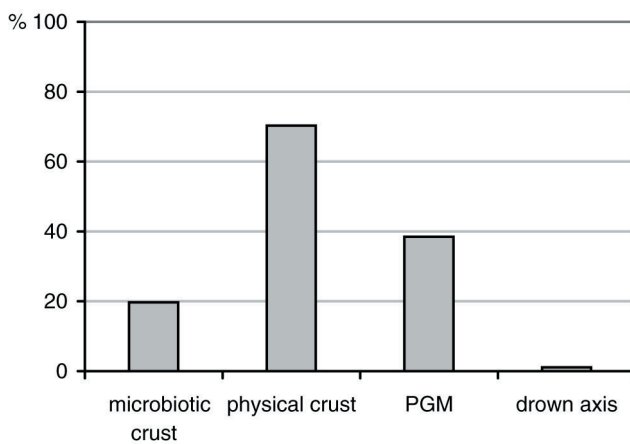


Fig. 3.9: Amount of microbiotic and physical crusts, phytogenic mounds (PGM) and down axis [%] in the whole Koeroegabvlakte (silty plain), northern Richtersveld.

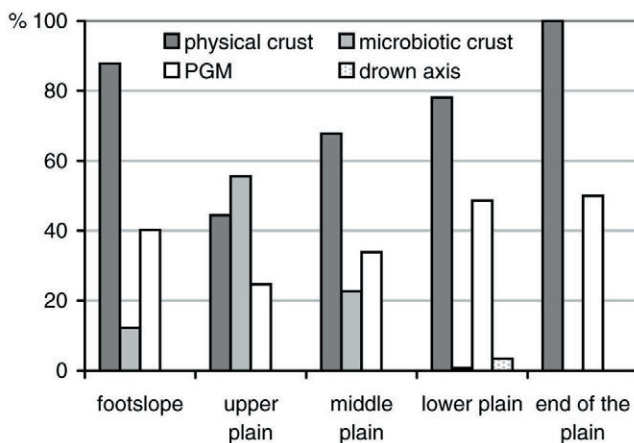


Fig. 3.10: The erosion parameter along a descending gradient from the footslope to the end of the silty plain, Koeroegabvlakte, northern Richtersveld. The amount of the parameter is given in %.



## 12 Slope habitats of the Succulent Karoo within the mountain area

Sub-order: *Tylecodon paniculatus* - *Osteospermum armatum* sub-ord. prov.

Diagnostic species: *Tylecodon paniculatus*, *Osteospermum armatum*, *Salvia gariensis*, *Rhus populifolia*, *Antimima watermeyeri*, *Pentzia spinescens*, *Euryops multifidus*, *Dyerophytum africanum*, *Tylecodon wallichii* s. *eckklonianus*, *Galenia dregeana*, *Berkheya fruticosa*, *Tylecodon orbiculata* v. *orbiculata*, *Ruschia senaria*, *Ozoroa dispar*, *Euphrobia hamata*, *Othonna arbuscula*, *Microlooma incanum*, *Arenifera stylosa*, *Dianthus namaensis*, *Berkheya spinosissima* s. *namaensis* v. *argentifolia*, *Polygala virgata* and *Antimima* S. *Clavipes\_ kahn*

General aspect: This part of the Richtersveld is the most diverse with regard to species and habitat richness. The escarpment joins the Vandersterrberg, Stinkfonteinberge and Goariëp mountains and reaches over 1000 m a.s.l. Due to their still high elevation of 900 to 1000 m a.s.l., the adjacent Koeroëgab mountains to the east were regarded as part of the escarpment. The western Gariëp mountains border to the north. Favourable parts of it were also counted to the presently described sub-order according to its floristic composition although its elevation ranges between 200 and 600 m.

Floristic composition: The Numees - Helskloof region shows the highest species number of up to 44 per m<sup>2</sup> and is known to be a centre of endemism comparable to the Western Gariëp Centre. The summits of the escarpment, from 1000 m up-wards, are special owing to the appearance of Fynbos elements of the Cape Floristic Region. The subdivision of this sub-order follows the results of the differentiated table A. T4 and the synoptic table A. T7.

Topography: The habitat diversity is caused by the rocky surface of the slopes. Rocks and rock faces subdivide the slopes into microhabitats of different exposition and inclination, wind-sheltered or exposed. The distinctive drainage system subdivides the slopes themselves into different habitats on a macro scale. Deep craved ravines and broad dry riverbeds subdivide the escarpment ranges.

Geology: The Vandersterrberg - Stinkfonteinberge are made of schist on the leeward side and of quartzite (sandstone) on the seaward side. The Goariëp mountains is part of the Tatasberg Complex and consists of granite, which weathers to large, rounded boulders and rock faces. The Koeroëgab mountains are part of the Vioolsdrif Suite consisting of orange-brown granite-gneiss.

Soils: The mountain slopes contain only a small portion of soil material. The chemical analysis of the soils shows no remarkable differences to the soil properties within the whole mountain region. The footslopes have minimally higher NaCl values in some places (A. T13), nevertheless the values of salts and nutrients are very low. The mean number of stone content measures about 35 % with a maximum in the 2 - 10 mm fraction. The soils are all very fine-grained and comprise of high silty fine sand or sandy silt (Tab. 3.3).

Climatic aspects: The escarpment receives the most rain due to the ascending moist air masses from the west wind drift. The gap in the escarpment created by the Oragne River valley enables the fog and rain to enter the mountain massif. Due to the high elevation the air temperature can fall to 0°C during winter nights, frost is common.

Vegetation pattern and cover: The appearance of the slope vegetation within the Succulent Karoo is mainly characterised by dwarf shrubs, but it changes to a high soaring trees dominated formation where channels or dry riverbeds subdivide the slopes. The well-developed dwarf

shrub formation of up to 1 m height show the highest ground cover within the Richtersveld, up to 53 %. The characteristic leaf succulent chamaephytes occur with 61 %, whereas the phanerophytes appear with 16 % (Tab. 3.2) and reaches heights of up to 200 m.

Floristic composition: The vegetation of the Richtersveld Mountain District reaches the highest number of species, up to 44 per 100 m<sup>2</sup> in the Numees valley at the escarpment (Tab. 3.2). *Galenia dregeana* (MCh l su) and *Ruschia senaria* (MCh l su) are common on footslopes, gentle slopes (Inclination < 40 %) and plateaux of higher altitude frequently in the region of the Numeesberg, Helskloof, Paradysberg and Die Koi. *Pteronia ciliata* (MCh l su) appears at a higher altitude than the latter and colonise, for example, the plateau-like top of the Kodaspeak (984 m) of the Koeroegab mountains. Where the inclination is higher than 40 % *Tylecodon wallichii* s. *ecklonianus* (MCh l + s su), *Antimima watermeyerii* (MCh l su), *Osteospermum armatum* (MCh l su) and *Pentzia spinescens* (MCh) are frequently observed. The trees *Rhus populifolia*, *Ozoroa dispar* and *O. concolor* indicate the occurrence of channels of dry riverbeds. *Tylecodon paniculatus* (NP s + l su), *Dyerophytum africanum* (NP) and *Salvia gariepensis* (NP/MCh) show no preference to a specific elevation. They are able to resist the cold at high altitudes, but they are also found on the low altitudes of the western Gariep mountains. They are very strong competitors in the struggle for water resources and secure themselves favourable sheltered positions on high rock boulders and rock faces with crevices of high water storage mainly on southern exposures.

Distribution: *Galenia dregeana* is endemic to the Richtersveld Mountain District, whereas *Ruschia senaria* is restricted to the northern Richtersveld. *Monechma incanum* (MCh wind) has its distribution centre in the Sudano-Zambezian Region.

The group of mountain species restricted to the Richtersveld Mountain District

There are several species that occur predominantly on the slope habitats but within both floristic regions, Succulent Karoo and Nama Karoo Region (A. T7, frame). These are *Ceraria fruticulosa*, *Euphorbia chersina*, *Euphorbia gummifera*, *Zygophyllum prismatocarpum*, *Tetragonia reduplicata* and *Prenia sladeniana*. The leaf and stem succulent *Ceraria fruticulosa*, reaching altitudes of up to 1000 m, is the most common shrub in the mountains of the Richtersveld. Its distribution area is restricted to the Richtersveld Mountain District and the eastern and western Gariep. *Prenia sladeniana* is restricted to the Richtersveld Mountain District.

### 121 Seaward habitats of the escarpment range

Alliance: *Didelta spinosa* - *Helichrysum hebelepis* all. prov.

Diagnostic species: *Didelta spinosa*, *Helichrysum hebelepis*, *Montinia caryophylacea*, *Sarcostemma viminale*, *Crassula muscosa* v. *obtusifolia*, *Senecio corymbiferus*, *Dyospyros ramulosa*, *Crassula macowaniana* and *Crassula expansa*

General aspect: The escarpment extends from the Sandveld plains at about 300 to 1000 m. The summits form a plateau of up to 1 km in diameter undulated with several peaks before it descends to the east. The syntaxa of this alliance were observed, on the seaward side of the Vandersterrberg - Stinkfonteinberge with its summits and the Goariep mountains, which is situated in front of the latter. On the transition from the slope to the plateau at about 900 m the vegetation changes. Increasingly Fynbos elements are mixed under the species of the Succulent Karoo.

**Topography:** The central part of the escarpments downwards slope reaches an inclination of 75° to 90°, whereas the upper part, where the slope merges into the plateaux-like summits is gentler with an inclination of 30 to 40°. Rock ledges or smaller plateaux with the consistency of the bedrock often interrupt the downward slope.

**Geology:** The seaward side of the escarpment consists mainly of sandstone, the Goariep mountains of granite. Despite the different stone formations the matrix of the alliance described occurs on both. If the differentiation on the association scale goes back to a different mineral content of sandstone and granite is unclear. Probably the reason is to be found in the different weathering products of the granite into large rounded rock boulders and rock faces that also provide different habitat conditions.

**Climatic aspects:** The habitats of the escarpment profit the most from the south-western cyclonic rain in winter, because the escarpment is the first barrier, which causes the moist air masses to ascend. But the escarpment is also a barrier to the west winds and due to the high ascent the temperature amplitude is high. Therefore the species have to cope with strong winds and low as well as high temperatures.

**Vegetation pattern and cover:** Although the physiognomic type of the vegetation is patchy and open in several parts with a high rock and gravel cover it can be fairly dense where sufficient moisture and surface stability are provided.

**Floristic composition:** The plant communities described in the following sections occur on the escarpment but also, in some cases, appear further inland at a higher altitude. There are several differential species, which give the formation its typical habit. *Aloe ramosissima* (MiP l + s su) is a much-branched small tree with yellowish green leaves, which rises beyond the plant formation such as the phanerophyte *Ozoroa dispar*. *Senecio corymbiferus* (MiP l + s su), *Crassula macowaniana* (MCh l su) and *Dianthus namaensis* (MCh) are found on diverse microhabitats of rocky slopes such as in Numees. *Sarcostemma viminalis* (MCh s su) forms large clusters on steep slopes by means of saltatoric growth, directed down-slope mainly on north-west exposed slopes. On exposed rocky outcrops *Helichrysum hebelepis* (MCh) are settled together with *Indigofera* sp. nov. 22906 (MCh). The species mentioned are common throughout the vegetation of the escarpment but are almost absent from the summits. On the contrary *Didelta spinosa* (NP l su), *Montinia caryophyllacea* (NP) and *Diospyros ramulosa* (NP) indicate high altitudes in the Richtersveld. *Didelta spinosa*, for example, is found at 500 m on the escarpment whereas on the Tatasberg it appears only at an altitude of 1000 m.

**Distribution:** The leaf succulent nano-phanerophyte *Didelta spinosa* is distributed in the Succulent Karoo Region from the Olifant River on sandy plains to the Ai-Ais Nature Reserve on sheltered rock slopes with some appearances in the Eastern Gariep District. *Montinia caryophyllacea* appears at altitudes of 700 m. Adapted to a higher amount of rainfall it is a widespread tree occurring throughout the Cape Floristic, Succulent Karoo and Nama Karoo Region. It is found on mountains as well as frequently on plains, for example in Kaokoland. Whereas *Diospyros ramulosa* is a Nama Karoo species restricted to high mountains.

### 1211 Summit habitats of the escarpment with Fynbos elements

Association: *Galenia africana* - *Prenia pallens* ass. prov.

Diagnostic species: *Galenia africana*, *Pteronia glauca*, *Ceterach cordatum*, *Indigofera* sp. nov. 22906, *Tylecodon wallichii* s. *wallichii*, *Pelargonium echinatum*, *Bromus pectinatus*, *Annesorhiza* 106438, *Tripteris sinuata*, *Pelargonium crithmifolium*, *Prenia pallens* and *Eriocephalus africanus*

General aspect: The highest summit of the escarpment reaches 1360 m. The moist habitat conditions allow the occurrence of several Fynbos elements of the Cape Floristic Region. The association described occurs on the plateau-like summits and peaks beginning at about 900 m. The amount of relevés is low due to the less accessible altitude of the steep rocky slopes, hence the assessment of the vegetation grouping is unsure. To confirm their diagnostic validity, further records would be necessary.

Topography: The slopes are moderately inclined and vary between 0° and 40° from 900 m to the plateau. In some parts, the plateau has only a plain surface. Large rock boulders cover the plateau and steep bedrock outcrops interrupt the plain surface. Several higher peaks ascend from the plateau. The highest are the Vandersterrberg at 1363 m and the Cornellsberg at 1374 m.

Vegetation pattern and cover: The mean ground cover reaches the highest value with about 50 % (A. P8). The majority of the species occurring in this group are non-succulent (55 %). The summits show the highest amount of chamaephytes (70 %) and the lowest of phanerophytes (4 %), but the number of hemicryptophytes is comparatively high with 11 %. The geophytes are present with 4 % (Tab. 3.2, Fig. 3.8.d). The ground cover varies between 47 to 53 %, the highest value of the Richtersveld.

Floristic composition: In the southern Richtersveld the differential species *Galenia africana* (MCh I su) and the grass *Fingerhuthia africana* (H) are very common on plains and higher plateaus. It is suspected that this species indicates intensive grazing as they occur in high frequency where the stock number is also high (for example in the Steinkopf area). The appearance of *Galenia africana* and *Fingerhuthia africana* on the top of the escarpment could also be interpreted as evidence for grazing. As previously mentioned (chapter 1.3.2) the stock farmers of the Nama migrate from the Oragne valley in the mountainous Richtersveld after the winter rain. Also the top of the escarpment serves as popular pasture. For example, the broad plateau of the Vandersterrberg is accessible via the Helskloof on its northern exposure. In sheltered positions at the base of higher plants or on shaded rock faces ferns such as *Ceterach cordatum* are common. The genus *Pelargonium* is widespread throughout the mountainous region of the Succulent Karoo. *Pelargonium echinatum* and *P. crithmifolium* are able to climb that high up. The shift of *Didelta spinosa* from southerly exposed habitats at low altitudes to all aspects in the upper montane belt indicates increasing general humidity towards the summits. Several species show the, for Fynbos species, typical shape such as *Eriocephalus africanus* (MCh) and the pleasant-smelling *Pteronia glauca* (MCh) for example. Their leaves are ericoid shaped. The mean number of species comes to 27 per 100 m<sup>2</sup> (Tab. 3.2).

Distribution: The main distribution area of *Eriocephalus africanus* lies in the mountainous Cape Floristic Region and the Succulent Karoo Region, where it reaches its northerly border in the Richtersveld mountains. *Galenia africana* is widespread throughout the Succulent Karoo

with some appearances in the Nama Karoo. The other differential species *Prenia pallens* (MCh l su) occurs, such as *Tylecodon wallichii* s. *wallichii* (MCh l and s su), within the Cape Flora and the adjacent Succulent Karoo. The beautiful orange flowering *Tripteris sinuata* is distributed throughout the whole Succulent and Nama Karoo.

#### 12111 Summit habitats on high elevations, above 1200 m

Sub-association: *Elytropappus rhinocerotis* - *Merxmuellera dura* sub-ass. prov.

Plots: 10470, 10471 and 10472

Diagnostic species: *Elytropappus rhinocerotis*, *Merxmuellera dura*, *Euryops tenuissimus* s. *tenuissimus*, *Euphorbia francescae*, *Euryops dregeanus*, *Chrysocoma ciliata*, *Zygophyllum flexuosum*, *Euryops lateriflorus*, *Othonna arborescens*, *Thesium strictum*, *Stachys lamarckii*, *Thesium congestum*, *Cheilanthes robusta*, *Tylecodon rubrovenosus* and *Selago robusta*

The 'Elytropappus rhinocerotis - Merxmuellera dura sub-ass.' occurs over 1200 m and reaches the highest mean ground cover (53 %) of the whole Richtersveld (Tab. 3.2).

Floristic composition: The dominant grass *Merxmuellera dura* forms a striking contrast to the common shrub-land at this altitude. It is found on the plateau, where it creates dense meadows mixed with patches of *Elytropappus rhinocerotis*. It should be mentioned that the proportion of the family Asteraceae is, with 50 % of all found species, remarkably high (14 out of 28 species). The switch-shaped *Euryops dregeanus* (MCh/NP), *Euryops tenuissimus* s. *tenuissimus* (MCh/NP) and *Euryops lateriflorus* (MCh/NP) are represented in this high frequency only on the rockiest habitats of the summits, where the rock cover reaches 50 - 70 %. The fern *Cheilanthes robusta* prefers the northerly wind and partly insolation sheltered aspects. The therophyte meadow mostly consists of *Heliophila cornuta* v. *squamata*, *Stachys lamarckii*, *Felicia ovata* and *Felicia filifolia* s. *schaeferi*. *Selago robusta* (MCh) and *Tylecodon rubrovenosus* (MCh l + s su) are species of the Succulent Karoo that are restricted to higher altitudes. The species richness is, with 27 per 100 m<sup>2</sup> (mean species number), also the highest of the whole Richtersveld apart from the Numees mountains (Tab. 3.2).

Distribution: The differential species *Elytropappus rhinocerotis* (MCh/NP), *Merxmuellera dura* (H), *Zygophyllum flexuosum* (MCh l su), *Othonna arborescens* (MCh l su) and *Thesium strictum* (MCh) have their distribution centre in the Cape Floristic Region. *Chrysocoma ciliata* (MCh) is common mainly in the Nama Karoo and the Sudano-Zambezi Region (eastern South Africa) but also occurs in the Cape Floristic Region. The only Euphorbiaceae in this community, apart from *Euphorbia chersina*, *Euphorbia francescae*, is endemic to the Richtersveld.

#### 12112 Summit habitats on lower elevations, 900 - 1200 m

Sub-association: *Pteronia divaricata* - *Berkheya canescens* sub-ass. prov.

Plots: 10467, 10468 and 10469

Diagnostic species: *Pteronia divaricata*, *Berkheya canescens* and *Tripteris breviradiata*

The mountain belt below the summits is occupied by the 'Pteronia divaricata - Berkheya canescens sub-ass.'. *Pteronia divaricata* (MCh l su) is common on sandy plains throughout the Namaqualand except on the coastal plain of the Richtersveld. Here, further north, the required habitat conditions of this species are only present on the high mountains of the escarpment. *Berkheya canescens*

(MCh thorny leaf) mainly occurs in the Eastern Gariep District. It shows the drier aspect of the community on north and east exposures. The relevés were taken from the northern exposure of the Vandersterrberg.

### 1212 Granite habitats of the escarpment annex Goariep mountains, 500 - 900 m

Association: *Antizoma miersiana* - *Ruschia Tumidula\_black fruits* ass. prov.

Plots: 10070, 10071, 10072, 10073, 10074, 10075, 10076 and 10077

Diagnostic species: *Antizoma miersiana* and *Ruschia Tumidula\_black fruits*

General aspect: The '*Antizoma miersiana* - *Ruschia Tumidula\_black fruits* ass.' is observed on the west exposed slopes of the Goariep mountains, situated in front of the escarpment, between 500 and 900 m. This association is only found on the granite of the Goariep mountains within the study area. The only diagnostic species that occurs in this community, is *Antizoma miersiana*. *Ruschia Tumidula\_black fruits* is common on the coastal plain (111211). The amount of diagnostic features is poor, compared with the other communities on the escarpment.

Topography: The granite provides favourable habitats with regard to water storage and insolation shelter. The large rock boulders and rock faces and walls give a surplus of rain water for the soil pockets in deep rock crevices.

Vegetation pattern and cover: The vegetation canopy is very patchy due to the irregular arrangement of the rock boulders, rounded bedrock outcrops and steep rock walls. But within the gaps where substrate has accumulated the vegetation cover is dense with 49 % mean cover (Tab. 3.2) and reaches heights of 1.5 to 2 m.

Floristic composition: The differential species *Ruschia Tumidula\_black fruits* (MCh I su) mainly appears frequently in inner-coastal plain habitats (1112) and re-occurs on the Goariep mountains in rock shelters. Its main companions are *Indigofera pungens* (MCh) and *Leipoldtia weingangiana* (MCh I su). *Indigofera pungens* is rarely distributed, but is found mainly on the escarpment and in the Eastern Gariep District. The leaf succulent dwarf shrub *Leipoldtia weingangiana* is found here on the escarpments rocky slopes at 700 - 900 m as well as at lower altitudes (200 m) in the western Gariep (1214) on the south-western exposure (see further on). The community described is mixed up with several species that indicate high water storage. *Tylecodon paniculatus*, *Rhus populifolia*, *Dyerophytum africanum* and *Salvia garipensis* occur in high abundance in rock shelters, the roots sink into water deposits found in deep fissures between the large rounded granite rocks. Phanerophytes such as *Montinia caryophylacea* (NP), *Diospyros ramulosa* (NP), *Carissa haematocarpa* (MiP) and *Stoeberia frutescens* (MiP) dominate little ravines.

Distribution: *Antizoma miersiana* (NP) occurs throughout the Namaqualand mainly on rocky slopes in the shelter of rocks.

### 1213 Habitats of the Vandersterrberg - Stinkfonteinberge, 500 - 900 m

Association: *Crassula grisea* - *Ruschia elineata* ass. prov.

Plots: 5936, 5937, 5940, 5949, 7901, 7902, 10065, 10127, 10201, 10202, 10203, 10204, 10206, 10207, 10208, 10209, 10210, 10211, 10214, 10215, 10217, 10218, 10221, 10222, 10223, 10224, 10225, 10227, 10229, 10230, 10236, 10237, 10241, 10242, 10243, 10244, 10245, 10246, 10247, 10248, 10284, 10285, 10286, 10287, 10296 and 10297

Diagnostic species: *Crassula grisea*, *Ruschia elineata*, *Bulbine frutescens*, *Aloe pearsonii*, *Mitrophyllum clivorum*, *Acanthopsis spathularis*, *Tylecodon buchholzianus*, *Crassula muscosa* v. *muscosa*, *Stapelia garipeensis*, *Conophytum jucundum*, *Adromischus filicaulis* s. *filicaulis* and *Conophytum meyeri*

General aspect: The footslopes of the escarpment, from 500 up to 900 m a.s.l., at the Numees mountains including Helskloof and Paradys mountain complex, are characterised by a dwarf shrub-land.

Topography: The habitat of this community is diverse in terms of exposure, relief energy, stone formation (quartzite, dolomite, tillites) and surface: high rock faces alternate with rocky sites covered with stones and chunks or with gravel surfaces in a confined space.

Vegetation pattern and cover: Due to the relatively low ground cover of 23 % and the low height of the vegetation cover (up to 0.5 cm), the dwarf shrub-lands looks more inconspicuous (A. P7). Only *Aloe ramosissima* (MiP) and *Ozoroa dispar* (MiP/NP), protruding above the dwarf shrubs, give a change in the appearance. One would not expect such plant diversity, which is characteristic for this association.

Floristic composition: This association is the most diverse of the Richtersveld, up to 44 species in 100 m<sup>2</sup> were found in the Numees valley (Tab. 3.2). The large families Mesembryanthemaceae and Crassulaceae that are significantly represented with 52 % and 21 %, supply the most endemics. The greyish-red coloured differential species *Crassula grisea* (MiCh I su) with the highest constancy (70 %) has a rather inconspicuous appearance reaching heights of only 5 to 15 cm. The climber *Ruschia elineata* (MCh I su) and *Bulbine frutescens* (G I su) are differential species determining the association with an abundance of 50 - 60 %. *Tylecodon buchholzianus* (MCh s + I su) and *Mitrophyllum clivorum* (MCh I su) by their frequent appearance characterise the stand. *Mitrophyllum clivorum* is special for its protecting strategy against transpiration. The existing leaf pair protects the growing leaves inside. When the older pair dies the younger leaves push their way free, still protected by the faded leaf pair. *Aloe pearsonii*, a concise appearance near the Helskloof, forms extended clusters caused by a high vegetative reproduction, which is unique throughout the Namaqualand. In spite of occurring in the western part of the Richtersveld, where the rain falls mainly in winter, the flowering time is in summer. The frequent geophytes are *Bulbine frutescens*, *Trachyandra bulbinifolia*, *Albuca spiralis* and *Gethyllis namaquensis*. The annual meadow consists mainly of *Didelta carnosa* v. *carnosa*, *Gorteria diffusa*, *Heliophila trifurca*, *Ursinia cakilefolia* and *Schismus barbatus*. The companions *Asparagus capensis* (MCh I fil), *Tetragonia fruticosa* (MCh I su) and *Lycium cinereum* (MCh frut), that occur on the coastal plain of the Sandveld, such as *Zygophyllum cordifolium*, climb up the foothills of the escarpment. *Zygophyllum cordifolium* (MiCh I su) occurring with the highest constancy, such as *Crassula grisea* (70 %), also distinguishes the community on the coastal plain close to the coast, the 'Zygophyllum clavatum - Euphorbia brachiata ass.' where it occurs with a constancy of 80 % (1211). Together with *Berkheya fruticosa* (MCh I thorny), *Monechma incanum* (NP), *Prenia sladeniana* and others, the companions mentioned are linked to the association on the south facing slopes of the Koeroegab (12211). Whereas *Tylecodon reticulatus* (s (thorny) + I su), *Antimima* S. *Clavipes\_kahn* (MCh I su), *Cotyledon orbiculata* v. *orbiculata* (MCh I su), *Crassula muscosa* v. *rigida* (MCh I su) and *Polygala virgata* (MCh frut) are companions which join up with the association on the north-east facing slopes of the Koeroegab (12213). *Astridia speciosa*, *Othonna opima* and *Othonna*

*arbuscula* (MCh s + l su) only occur at the escarpments low altitude. Hence these species are also found in the western Gariep at 200 m within the 'Acrotome pallescens - Astridia alba ass.' described below (1214).

Distribution: Due to the high species diversity this region is also a centre of endemism. *Arenifera stylosa* (MCh l su), *Astridia speciosa* (MCh l su), *Stapelia gariepensis* (MiCh), *Othonna opima* (MCh s + l su), *Prenia sladeniana* (MiCh l su) and *Rhynchosia emarginata* (MCh) are endemic to the Richtersveld. *Crassula macowaniana* (MCh l su), *Acanthopsis spathularis* (H), *Dianthus namaensis* (H), and *Aloe pearsonii* (NP l su) are restricted to the Namaqualand. The small compact *Crassula grisea* (NCh l su) with its narrow packed leaves is endemic to the northern Namaqualand.

On the highest peaks of the Koeroegab the 'Crassula grisea - Ruschia elineata ass.' re-occurs at the higher altitude of the Peilkop at 625 - 700 m and on the Kodaspeak at 850 - 950 m.

#### 1214 Habitats of the western Gariep mountains; 100 - 200 m, south-west facing slopes

Association: Acrotome pallescens - Astridia alba ass. prov.

Plots: 6114, 6115, 6116, 6121, 6123 and 6124

Diagnostic species: *Acrotome pallescens*, *Astridia alba* and *Othonna opima*

General aspect: The western Gariep mountains form a gap in the escarpment ridge, which stretches from north-west to south-east. In a strong contrast it combines species of the humid westerly escarpment with the drought-resistant species of the inner-mountain region within a confined space. There is a strict division of the two communities: The 'Acrotome pallescens - Astridia alba ass.' (described in this section) occurs on the more humid south-west exposed slopes whereas the 'Zygophyllum microcarpum ass.' (2212) is restricted to the north-east facing slopes (described below).

Topography: The habitat of both communities is a feature of high rock faces and chunks consisting of granite. Hence sheltered sites and deep crevices are available which are filled with silty fine sand with a high water storage capacity. The habitat conditions are suitable, although the western Gariep is situated at 100 - 400 m and reaches just 600 m on the border to the eastern Gariep.

Geology: The eastern part of the western Gariep consists of the younger Namaqualand basement granites (Vioolsdrif Suite), the smaller western part belongs to the Gariep Complex as does the escarpment range.

Climatic aspects: Due to the gap in the high mountain ridge of the escarpment, fog is able to reach the western Gariep along the Oragne River valley giving episodically higher air humidity than arising in eastern Gariep. Nevertheless, due to the low elevation, the temperature can reach high values of up to 50°C.

Vegetation pattern and cover: The 'Acrotome pallescens - Astridia alba ass.' has a mean ground cover of 3 %, in contrast to the 'Zygophyllum microcarpum ass.' with 2 % (Tab. 3.2). The high presence of leaf succulents, 63 % (A. T7) within the community shows the relationship to the Succulent Karoo Region.

Floristic composition: The association is similar to the 'Crassula grisea - Ruschia elineata ass.' even though most of the species occurring at high altitudes are absent. Both communities share the species *Astridia speciosa* (MCh l su), *Othonna opima* (MCh s + l su), *Othonna*



*arbuscula* (MCh s + l su), *Microlooma incanum* (MCh wind) and *Conophytum jucundum* (NCh l su). *Senecio corymbiferus* (MCh s + l su), *Cotyledon orbiculata* v. *orbiculata* (MCh l su), *Galenia dregeana* (MCh l su) and *Trachyandra bulbinifolia* (G l su), which characterise the escarpment syntaxa, are sprinkled in. Even *Leipoldtia weigangiana* (MiCh l su), a species that occurs on the Goariep mountain complex, appears. The presence of *Euphorbia chersina* (MCh s su), *Euphorbia ephedroides* (MCh s su), *Zygophyllum prismatocarpum* (NP l su) and *Stoeberia beetzii* (MCh l su) underlines the relationship to the Succulent Karoo. *Sarcocaulon crassicaule* (NCh s su), *Hoodia alstonii* (NP s su pach) and *Pelargonium desertorum* (MCh s su) are related to the Koeroegab, such as *Schwantesia herrei* (MiCh l su), that appears on the north facing slopes of the Koeroegab (12213). However the vicinity to the Nama Karoo communities is perceptible with the companions *Commiphora capensis* (NP s su pach), *Ceraria namaquensis* (NP s + l su), *Ruschia abbreviata* (MCh s + l su) and *Pachypodium namaquanum* (NP s su pach l su) occurring at a low frequency (22). In the shelter of rock faces with reduced insolation *Tylecodon paniculatus* (NP s su pach l su), *Euryops multifidus* (MCh), *Dyerophytum africanum* (NP rut) and *Salvia garipensis* (MCh) appear (2) within the 'Acrotome palescens - Astridia alba ass.'. The mean number of species has 14 per 100 m<sup>2</sup> in contrast to the 'Zygophyllum microcarpum ass.' with 7 per 100 m<sup>2</sup> (Tab. 3.2).

Distribution: The highly frequent *Acrotome palescens* (MCh) is restricted to the Namib Subdomain of the Nama Karoo Region with some occurrence in the Western Gariep Centre of the Succulent Karoo. The occurrence of the genus *Astridia* (MCh l su) is limited to the northern Succulent Karoo Region, showing the membership to the Southern Namib District.

## 122 Leeward habitats of the escarpment range; 450 - 950 m

Alliance: *Chrysocoma puberula* - *Menodora juncea* all. prov.

Diagnostic species: *Chrysocoma puberula*, *Menodora juncea*, *Nymanina capensis*, *Hoodia gordonii*, *Wahlenbergia patula* and *Leipoldtia schultzii*

The inner-mountain basin Koeroegabvlakte is surrounded by mountain summits of 600 (E) up to 980 m (W, Peilkop) elevation. The basin level measures 400 (E) - 600 m (W). The 'Chrysocoma puberula - Menodora juncea all.' occurs up to 900 m. Upper summits are colonised by the 'Crassula grisea - Ruschia elineata ass.' (1213).

Topography: The habitats of the Koeroegab are comparable with those of the western Gariep.

Geology: The mountains of Koeroegab belong to the granite-gneiss of the Violsdrif Suite such as the western Gariep.

Climatic aspects: Due to relatively high altitudes, compared to the western and eastern Gariep, the rocky habitats of the Koeroegab receive seasonal rain from the west wind drift. The air temperature is still moderate due to the high elevation, despite the leeward position and the increasing proximity to the hot eastern Gariep region.

Vegetation pattern and cover: The different slope aspects of this mountain cycle are very obvious, and are expressed by the ground cover values of the vegetation canopy. The south-eastern exposed habitats show a high mean ground cover of 28 %, whereas the north-western exposed habitats are clearly less covered with 14 % (Tab. 3.2).

Floristic composition: The dwarf shrub formation of the Succulent Karoo is mixed with several nano-phanerophytes and chamaephytes of the Nama Karoo e.g. *Euphorbia guerichana*

(NP s frut to su), *Menodora juncea* (MCh) and *Aptosimum spinescens* (MiCh leaf thorny). The notably constant (84%) *Tetragonia fruticosa* (MCh l su) is a typical leaf succulent shrub of the Succulent Karoo, which also occurs with a high frequency within the syntaxa along the coastal plain (Sandveld). The therophytes *Leysera tenella* and *Enneapogon scaber* are common on the Koeroegab mountains. They are accompanied by other therophytes such as *Didelta carnosus* v. *carnosus*, *Gorteria diffusa*, *Ursinia cackilefolia* and *Heliophila variabilis* with a high frequency. The north exposed slopes show a high mean number of species with 23 per 100 m<sup>2</sup> compared to the low cover density and are therefore higher than the south exposed slopes with 16 - 18 per 100 m<sup>2</sup> (Tab. 3.2). The reason can be seen in the close vicinity to the escarpment range of the northern slopes in contrast to the southern mountain ridge.

Distribution: The rare *Chrysocoma puberula* (MCh) is endemic to the Richtersveld mountains. *Menodora juncea*, which is also rare, comes from the east, the Nama Karoo side, such as the companions *Euphorbia guerichana* and *Aptosimum spinescens*. A second focus of the disjunctive distribution area of *Euphorbia guerichana* lies in the east of the Sudano-Zambezian Region. The association is found throughout the whole leeward side of the escarpment at an elevation of 450 - 950 m, e.g. Domorogh mountains, Abiqua mountains and Maerpoort mountains. Whereas the habitats, which are on the leeward side of the escarpment range, are additionally situated in the rain shadow of the Rosintjebos mountains, the Nama Karoo syntaxa replaces this association on similar elevations.

#### 1221 South exposed slope habitats

Association: *Cheilanthes capensis* - *Zygophyllum leptopetalum* ass. prov.

Plots: 5902, 5905, 5909, 5910, 5911, 5912, 5913, 5935, 5938, 5939, 5947, 5948, 5950, 5951, 5952, 5953, 5987, 5988, 5989, 5990, 5991, 5992, 5993, 5994, 6065, 6076, 6150, 6156, 6176, 6209, 6213, 6245, 10068, 10069, 10104, 10105, 10106, 10107, 10108, 10110, 10111, 10114, 10122, 10138, 10139, 10219, 10304, 10381, 10403 and 10406

Diagnostic species: *Cheilanthes capensis*, *Zygophyllum leptopetalum*, *Pteronia lucilioides* and *Hermannia gariepensis*

The association 'Cheilanthes capensis - Zygophyllum leptopetalum' colonises moist south facing aspects (A. P10). *Zygophyllum leptopetalum* (MCh l su), *Pteronia lucilioides* (NP rut) and *Hermannia gariepina* (MCh) are distributed in the Nama Karoo. The fern *Cheilanthes capensis* is common in the Cape Floristic Region expanding to the north along the escarpment. *Asparagus capensis* (MCh), *Berkheya fruticosa* (MCh), *Prenia sladeniana* (MCh l su), *Arenifera stylosa* (MCh l su) and *Rhynchosia emarginata* (MCh), the companions of the 'Crassula grisea - Ruschia elineata ass.' (1213) re-occur on the south exposures of the Koeroegab and give it the typical appearance of the Succulent Karoo.

#### 1222 West exposed slope habitats

Association: *Ruschia brevibracteata* - *Lycium hirsutum* ass. prov.

Plots: 5903, 5904, 5906, 5907 and 5908

Diagnostic species: *Ruschia brevibracteata* and *Lycium hirsutum*

On west exposed slopes *Ruschia brevibracteata* (MCh rept l su) forms conspicuous patches. This

aspect can also be seen on the Rooiberg's western slope further east at 830 m. The appearance of *Ruschia brevibracteata* and *Lycium hirsutum* is the reason for the separation of this group into its own association. Otherwise this group shows a transition position between southern and northern exposure discernible by the occurrence of the following species: *Hermannia gariepina* (S) and *Tripteris polycephala* (N).

### 1223 North-east exposed slope habitats

Association: *Tripteris polycephala* - *Crotalaria meyeriana* ass. prov.

Plots: 5914, 5915, 5916, 5917, 5918, 5919, 5920, 5921, 5922, 5923, 5924, 10115, 10116, 10117, 10136, 10140, 10150, 10151, 10295, 10402, 10404 and 10405

Diagnostic species: *Tripteris polycephala*, *Tylecodon reticulatus*, *Schwanthesia herrei*, *Crotalaria meyeriana*, *Stipagrostis anomala* and *Aristida adscensionis*

The '*Tripteris polycephala* - *Crotalaria meyeriana* ass.' is the north facing aspect at Koeroegab. *Tripteris polycephala* (T/Ch) is a seldom species of the lower Orange River valley, whereas the distribution focus of *Crotalaria meyeriana* (MCh) is located in the Western Gariep Centre. The differential species *Eriocephalus ericoides* and *Salsola zeyheri*, occurring with a high abundance (50 %), have a wide distribution area from the Nama Karoo to the Sudano-Zambezian Region. The higher insolation causes a lower mean ground cover (14 %) than on the southern exposures with 28 % (Tab. 3.2). Therefore more therophytes occur with a high constancy (up to 80 %) such as *Trianthema triquetra*, *Lotononis strigillosa*, *Aristida adscensionis* and *Lotononis falcata*. The latter three are also common on the Koeroegabvlakte. There is a link to the escarpment association '*Crassula grisea* - *Ruschia elineata*' (1213): *Tylecodon reticulatus*, *Antimima* S. *Clavipes* kahn, *Cotyledon orbiculata* v. *orbiculata*, *Crassula muscosa* v. *rigida* and *Polygala virgata*. *Schwanthesia herrei*, showing the connection to the western Gariep association '*Acrotome pallescens* - *Astridia alba*', reaches a high constancy (62,5 %). On the lower parts of the slopes *Sarcocaulon crassicaule*, *Hoodia alstonii* and *Pelargonium dessertorum* re-appear but at this altitude mostly on the northern exposure described here (see 1214).

## 2 Habitats of the Nama Karoo

Order: *Sarcocaulon crassicaule* - *Blepharis furcata* ord. prov.

Diagnostic species: *Forsskaolea candida*, *Blepharis furcata*, *Aptosimum spinescens*, *Chrysocoma schlechteri*, *Hermannia stricta*, *Zygophyllum retrofractum*, *Kissenia capensis* and *Trianthema triquetra*

General aspect: The part of the Nama Karoo that borders the Succulent Karoo in the north-east of the Richtersveld is called the Eastern Gariep District and is represented by the following taxa: *Pachypodium namaquanum*, *Ceraria namaquensis*, *Sisyndite spartea* and *Schotia afra*. *Aloe dichotoma*, *Euphorbia phylloclada*, *Euphorbia gariepina* and *Sesuvium sesuoides* show the link between the desert landscape of the eastern Richtersveld and the dry inland desert of the northern and Central Namib (Namib Subdomain). The relationship to the inland scrubland of the Nama Karoo consists of the taxa *Calicorema capitata*, *Kissenia capensis* and *Parkinsonia africana* (Jürgens 1991).

Topography: The eastern Gariep mountains are not as high as the Vandersterrberg - Stinkfonteinberge or the Rosintjebos mountains (1000 - 1300 m). The summits directly at the Oragne River valley reach 300 m, further west 800 m. Only the Rooiberg (882 m) and Tatasberg (1026 m) are higher.

Climatic aspects: Precipitation is low on account of lying in a gap between winter rain to the west and summer rain to the east. Even fog is not able to reach the upper Orange River valley; hence the air humidity is low. The air temperature increase is correlated to the altitude decrease in the Orange River valley.

Vegetation pattern and cover: The majority of the Nama Karoo species are adapted to episodic but higher precipitation (up to 400 mm/year). Therefore they are mainly stem succulent or evergreen stem and leaf succulents able to store water quickly when it rains a lot over a short period. In the Eastern Gariiep District the stem succulent reaches 28 % compared to 14 % in the Succulent Karoo (Tab. 3.2, Fig. 3.8.b). If the species are not adapted to episodic or low precipitation they require water throughout the whole year for example trees such as *Parkinsonia africana*. As a result of this they depend on channels and drainage lines in this dry region (Phreatophytes). Compared with the dwarf shrub-land of the Succulent Karoo the species occurring in this desert-like part of the Richtersveld form a dry scrubland.

Floristic composition and distribution: There are a lot of species that are mainly distributed in the Nama Karoo Region and further east in the Sudano-Zambezian Region. However, the common *Forsskaolea candida* (H/Ch) is widespread throughout the whole Nama Karoo with some occurrence in the Succulent Karoo. *Hermannia stricta* (MCh), mostly found at lower altitudes, and *Acantopsis disperma* (T) have their main distribution area in the Richtersveld but it stretches along the Orange River to the east with some occurrence in the Southern Karoo. *Blepharis furcata* (MiCh with thorny leaves) is distributed with a low occurrence throughout the Nama Karoo Region with the focus on the Eastern Gariiep District. If the rain reaches the far east of the Richtersveld episodically then the annuals are able to germinate. Therophytes of the genera e.g. *Dimorphotheca*, *Ursina*, *Osteospermum* and *Gazania* but also *Geigeria vigintiquamea* and *Helichrysum roseo-niveum* flower briefly after the rain. *Trianthema triquetra* is the most common therophyte of the Eastern Gariiep District, which penetrates, with some other species, deep into the Succulent Karoo. For example *Kissenia capensis*, which is found on rocky slopes as well as on sandy flood plains.

## 22 Slope habitats of the Nama Karoo within the mountain area

Sub-order: *Kleinia longiflora* - *Hermannia stricta* sub-ord. prov.

Diagnostic species: *Kleinia longiflora*, *Hermannia stricta*, *Sarcocaulon crassicaule*, *Tetragonia reduplicata*, *Eriocephalus ericoides*, *Indigofera nigromontana* and *Enneapogon scaber*

General aspect: The dry shrub formation described in this section, differs from the dwarf shrub-land of the Succulent Karoo with regard to lower diversity and canopy cover. Due to the low vegetation cover the subdivision of the dry shrub-land into vegetation units is aggravated. Differential species of the highest unit are absent in some relevés of the lower units. The differentiated tables A. T5 and A. T7 give the results for the subdivision of this sub-order.

Topography and climatic aspects: The eastern Gariiep receives only episodic rain in contrast to the western part of the Richtersveld. The escarpment ridge is a barrier to the cyclonic precipitation in winter. Hence, the majority of the rain falls as the air masses ascend the steep escarpment; it only rarely reaches the eastern Gariiep. Also the convective precipitation, characteristic for the inner part of the continent, rarely occurs. The eastern Gariiep is situated in a precipitation gap, where only episodic thunderstorms appear in summer

with heavy rain during short periods. The result of these events is high surface drainage and flooding of the dry riverbeds and plains, while the surface sediments get washed out. Therefore the shape of the mountains looks craggier and rougher than the western part of the Richtersveld.

**Geology:** The western part consists of Vioolsdrif Suite granite and the majority of the eastern part is made of lava of the Orange River Group. The Tatasberg Complex also consists of granite but medium-grained non-porphyrific granite that weathers to large rounded chunks and extended rock faces. The Tatasberg Complex re-occurs at the Goariep mountains.

**Soils:** The soils are shallow and restricted to rock fissures and crevices of the rocky surface as throughout the whole mountain region. The stone content is remarkably higher than those of the western slope habitats. The fine-grained silty soils show no subdivision into different layers. The chemical analysis revealed no remarkable differences between the slope habitats of the mountain region (Tab. A. 13).

**Vegetation pattern and cover:** The mean ground cover decreases from the western part of the eastern Gariep to the Orange River valley from 11 to 2 % (Tab. 3.2). Near the valley the species occur locally at distances of 100 to 150 m or are completely absent. There is a subdivision of the vegetation along the slope. The footslopes are covered with drought-resistant species such as the species of the 'Calicorema squarosula ass.' or the 'Euphorbia virosa - Euphorbia gariepina ass.' (2112, 2215) and the upper parts show the communities of the 'Ceraria namaquensis - Aloe dichotoma all.'.

**Floristic composition:** The mean number of species reaches 3 - 8 per 100 m<sup>2</sup> (Tab. 3.2). The decreasing mean number of species from the western (7 - 8) to the eastern part (3 - 4) of the eastern Gariep mountains is very conspicuous. The widespread species of the mountain region such as *Ceraria fruticulosa* (MCh/NP s + l su), *Euphorbia gummifera* (NP s su), *Euphorbia guerichana* (NP), *Kleinia longiflora* (NP s su), *Zygophyllum prismatocarpum* (NP s + l su) and *Indigofera nigromontana* (MCh) are intermingled in the western part and are absent in the lower Orange River valley.

**Distribution:** *Kleinia longiflora* (NP s su) comes from the east and is distributed in the Nama Karoo and the Sudano-Zambezian Region. *Hermannia stricta* is a typical Nama Karoo species with appearances in the Richtersveld Mountain District and Western Gariep Cycle. *Sarcocaulon crassicaule* (NCh s su) is a Nama Karoo species with a high frequency but also appears in the Succulent Karoo (Richtersveld).

## 221 Habitats of the Gariep region and the lee-ward side of the escarpment range

Alliance: *Ceraria namaquensis* - *Aloe dichotoma* all. prov.

**Diagnostic species:** *Ceraria namaquensis*, *Aloe dichotoma*, *Commiphora capensis* and *Peliosotomum leucorrhizum*

**Vegetation pattern and floristic composition:** *Ceraria namaquensis* dominates the association preferring the sheltered rock sites with a higher provision of water (A. P15). *Commiphora capensis* occurs frequently and regularly on the more favourable habitats of the western part of the eastern Gariep but is rare or absent in the approaches to the eastern Orange valley. *Aloe dichotoma* is a frequent but rare diagnostic species but more widespread than *Commiphora capensis* within the association. Along the transition zone of Succulent Karoo and Nama Karoo these Nama Karoo elements are meshed with species of the dwarf

shrub formation (2211). The three species mentioned are stem succulents in response to the episodic precipitation. Additionally *Ceraria namaquensis* and *Aloe dichotoma* are also leaf succulent. But *Ceraria namaquensis* has, such as *Commiphora capensis*, deciduous leaves (in the case of *Commiphora capensis* also deciduous axis) that gives the plant the opportunity to reduce transpiration during the hot summer period.

Distribution: *Ceraria namaquensis* is restricted to the desert and semi-desert regions in the Orange River valley between the Richtersveld and the Pofadder-Upington vicinity. Therefore both, *Ceraria namaquensis* and *Commiphora capensis*, floristically characterise the Eastern Gariep District. *Commiphora gracilifrons* with the same distribution area and similar look of *Commiphora capensis* (except for the different leaf-shape) is scattered and rare in this association. *Aloe dichotoma* is a link between the desert to semi-desert region of the Richtersveld and the desert landscape of the Central and Northern Namib.

### 2211 Favourite habitats in rock shelters

Association: *Pachypodium namaquanum* ass. prov.

Plots: 6109, 6119, 6120, 6142, 6147, 6153, 6154, 6157, 6158, 6159, 6208, 6210, 6211, 6212, 6218, 10036, 10049, 10052, 10057, 10059, 10060, 10066, 10109, 10112, 10113, 10298, 10302, 10328, 10361, 10401, 10407, 10408, 10409, 10411, 10463 and 10466

Diagnostic species: *Pachypodium namaquanum*

This association is the richest with regard to the mean number of species (up to 14/100m<sup>2</sup>) and cover percentage (11 %) and shows the highest similarity with the communities of the Succulent Karoo (Tab. 3.2). It is found in a close patchwork with the 'Acrotome pallescens - Astridia alba ass.' in the western Gariep (1214) and the 'Chrysocoma puberula - Menodora juncea all.' (122) in the northern surroundings of the Koeroegab. The association normally appears at altitudes between 200 and 500 m but it reaches up to 1000 m and forms a far distant exclave, due to the rain shadow on the lee-ward side of the escarpment and the Rosintjebos mountains. *Pachypodium namaquanum* (MiP s + l su) is, such as *Ceraria namaquensis*, restricted to the desert and semi-desert regions within the Orange River valley. *Pachypodium namaquanum* is also a companion of the 'Acrotome pallescens - Astridia alba ass.' in the Pokkiespram Region (western Gariep). *Eriocephalus ericoides* (MCh/NP), *Othonna opima* (MCh s + l su) as well as the leaf succulent chamaephyte *Ruschia brevifolia* accompany this association.

### 2212 Habitats of the western Gariep mountains; 100 - 200 m, north-east facing slopes

Association: *Zygophyllum microcarpum* ass. prov.

Plots: 6107, 6108, 6110, 6111, 6112, 6113, 6122, 6125, 6126, 6127, 6128, 6129, 6133, 6140, 6141, 6148, 6167, 6185, 10037, 10043, 10044, 10045 and 10064

Diagnostic species: *Zygophyllum microcarpum*

In the western Gariep region a strong contrast between the north-east and south-west expositions exists, with reference to the response of the vegetation to extremely different habitat conditions. The 'Zygophyllum microcarpum ass.' is restricted to the north facing slopes with higher insolation and air temperature, whereas the 'Acrotome pallescens - Astridia albida ass.' (1214) requires the moist south-west exposed slope habitats (altitude 10 to 400 m). *Zygophyllum microcarpum* (MCh

l su) is widespread throughout the Nama Karoo and finds its north-western border in the eastern Richtersveld. *Aloe gariensis* (MCh l su), appearing on steep and rocky slopes, is restricted to the Oragne River valley. *Peliostomum virgatum* and *Stipagrostis ciliata* and occasionally *Euphorbia gummifera*, are frequent companions.

#### 2213 Habitats of the eastern Gariep mountains; 50 - 300 m, south-west facing slopes

Association: *Brownanthus nucifer* - *Ruschia abbreviata* ass. prov.

Plots: 6117, 6118, 6135, 6137, 6139, 6143, 6145, 6146, 6155, 6160, 6166, 6219, 6220, 6234, 6235, 6236, 6237, 6239, 6240, 6259, 6293, 6294, 6298, 10011, 10014, 10041, 10042, 10050, 10054, 10063, 10300, 10301, 10303, 10305, 10307, 10311, 10313, 10314, 10319, 10322, 10324, 10326, 10334, 10336, 10338, 10340, 10342, 10347, 10348, 10353, 10360, 10363, 10366, 10372, 10373, 10375, 10376, 10413, 10423, 10426, 10429, 10430, 10439, 10444 10461 and 10464

Diagnostic species: *Brownanthus nucifer* and *Ruschia abbreviata*

The 'Brownanthus nucifer - *Ruschia abbreviata* ass.' of the eastern Gariep tolerates drier conditions than the previous units. In the north it penetrates the western Gariep communities where it colonises the drier footslopes up to 200 m below the beginning of the 'Acrotome pallescens - *Astridia alba* ass.' (1214). The footslopes are dry because they are combined with the extrazonal hot Orange River valley system. *Eberlanzia schneiderana* (MCh l su), the pioneer *Hyperthelis salsoloides* (Mi-Ch l su) and *Trianthema triquetra* (T l su) are frequently accompanied. In the west it borders on the 'Pachypodium namaquanum ass.' (Abiquavlake at 395 m). With increasing air temperature further east, within the catchments area of the Gannakouriep, it alternates with the 'Euphorbia decussata ass.' (2214). Whereas the 'Brownanthus nucifer - *Ruschia abbreviata* ass.' prefers the south-western exposure the 'Euphorbia decussata ass.' is restricted to the north-east facing slopes (altitude limit: 300 m). *Brownanthus nucifer* (MCh s + l su), which is endemic to the Eastern Gariep District, creates broad clusters according to a high vegetative productivity, so that those belonging to the 'Ceraria namaquensis - *Aloe dichotoma* all.' are less obvious in some places.

#### 2214 Habitats of the eastern Gariep mountains; 200 - 700 m, mostly north-east facing slopes

Association: *Euphorbia decussata* ass. prov.

Diagnostic species: *Euphorbia decussata*

Further east *Euphorbia decussata* (MCh s su) joins the dry scrubland. *Hermannia stricta* and the two diagnostic species of the alliance, *Ceraria namaquensis* and occasionally *Aloe dichotoma*, are the only companions until *Commiphora capensis* appears at an elevation of 400 m and higher. *Euphorbia decussata* is common in the whole Orange River valley up to the Upington vicinity. This association has two different variations depending on altitude.

#### 22141 Dry habitats without high altitude species

Typicum: *Euphorbia decussata* typ. nov.

Plots: 5932, 6131, 6169, 6170, 6171, 6175, 6177, 6223, 6291, 10007, 10030, 10032, 10033, 10039, 10040, 10046, 10053, 10056, 10062, 10306, 10330, 10332, 10335, 10337, 10339, 10341, 10343, 10345, 10346, 10349, 10352, 10354,

10359, 10365, 10367, 10368, 10369, 10370, 10371, 10377, 10378, 10380, 10399, 10435, 10438, 10446, 10447, 10448, 10452, 10453, 10456, 10459 and 10465

Diagnostic species: *Euphorbia decussata*

Is found in the catchments area of the Gannakouriep where it is restricted to the northern exposures in contrast to the 'Brownanthus nucifer - Ruschia abbreviata ass.' on southern exposures (2213). The mean number of species increases from 4 species, within the *Euphorbia decussata* typicum, to 8 species within the 'Brownanthus nucifer - Ruschia abbreviata ass.' (Tab. 3.2).

#### 22142 Favourite habitats at higher altitudes between 400 - 700 m

Sub-association: *Ruschia spinosa* sub-ass. prov.

Plots: 6225, 6243, 6244, 6246, 6247, 6248, 6249 and 10035

Diagnostic species: *Ruschia spinosa*

From 450 m a.s.l. up-wards the mean ground cover increases from 8 to 10 % and the mean number of species rises from 4 to 8 species, due to the re-appearance of the mountain elements with a higher requirement for humidity e.g. *Ceraria fruticulosa*, *Euphorbia gummifera*, *Euphorbia guerichana* and *Kleinia longiflora*. As an aspect of higher altitude a new species occurs, *Ruschia spinosa* (MCh thorny l su), also observed on the west slope of the Vandersterrberg. The leaf succulent *Ruschia spinosa*, with thorny inflorescence, is widespread throughout the whole Nama Karoo and further east in the Sudano-Zambezi Region.

#### 2215 Habitats of the eastern Gariep mountains close to the Oragne valley; 50 - 500 m, mostly north facing slopes

Association: *Euphorbia virosa* - *Euphorbia gariepina* ass. prov.

Plots: 6162, 6165, 6179, 6180, 6222, 6227, 6230, 6238, 6257, 6258, 6260, 6261, 6264, 6265, 6266, 6267, 6295, 6299, 6300, 10002, 10003, 10005, 10009, 10025, 10026, 10031, 10038, 10048, 10051, 10316, 10317, 10320, 10323, 10325, 10327, 10329, 10331, 10333, 10344, 10350, 10364, 10374, 10379, 10421, 10422, 10424, 10425, 10427, 10428, 10431, 10432, 10434, 10436, 10440, 10441, 10442, 10445 and 10460

Diagnostic species: *Euphorbia virosa* and *Euphorbia gariepina*

The hot upper Oragne River valley (eastern Gariep) is colonised by the '*Euphorbia virosa* - *Euphorbia gariepina* ass.' (A. P16). It penetrates deeply into the richer '*Ceraria namaquensis* - *Aloe dichotoma* all.' particularly via river valleys, where they form a mixture in the transition zone. *Euphorbia virosa* (NP s su) and *Euphorbia gariepina* (MCh s su) belong to the flora of the dry inland desert or semi-desert regions of the eastern Richtersveld (Namib Subdomain) linked with the desert regions of the Central and Northern Namib. The differential species of the '*Ceraria namaquensis* - *Aloe dichotoma* all.' are absent next to the Orange River valley. *Euphorbia virosa* appears in pure stands on steep slopes whereas *Euphorbia gariepina* occurs singly on footslopes or on gentle slopes and plateaux. This community has the lowest mean number of species (3) and a mean ground cover of only 3 % (Tab. 3.2). *Parkinsonia africana*, common on the inland scrubland of the Namib, occurs rarely on runnels within the '*Euphorbia virosa* - *Euphorbia gariepina* ass.'.



## 21 Habitats on gravelly flood plains and drainage lines

Sub-order: *Codon royenii* - *Trichodesma africanum* sub-ord. prov.

Diagnostic species: *Codon royenii*, *Trichodesma africana*, *Sesuvium sesuvioides*, *Pharnaceum croceum* and *Boscia albitrunca*

General aspect: The drainage system of the inner-mountain basins and the extended flood plains in the east e.g. the Springbokvlakte constitute a special habitat type. The plant communities are subject to rapid habitat changes in terms of soil movements by water floods. The drainage system of the western Richtersveld seasonally draws off the water volume that accumulates in the surrounding mountains after winter rains. Episodical thunderstorms in summer are able to trigger broad expanses of soil movements observable on the flood plains of the eastern Gariep. During these precipitation events water always flow different directions. In this way a habitat mosaic of different age and therefore different succession stages is developed. The essential examination of these succession processes is not part of the study on hand. Hence, the subdivision of this inhomogeneous vegetation type in phytosociological groups has to be understood as a first attempt (see the tables A. T6 and A. T7).

Topography: The sand-choked plains and valleys have a plain surface and a regular downwards slope with an inclination of 2 - 5°. The majority of the plains within the mountain region are gently concave. The drainage system is dendrite and the main stream flows down the deepest line of the plain slope. Within the more narrow valleys such as that of the Kouamsrivier in the western Gariep, the main stream meanders. In some places the main stream has carved deeply into the plain, so that the sediment layers build up walls beside the main stream. This phenomenon can be observed at the end of the Koeroegabvlakte.

Geology: The material, which forms the surface of the plains and valleys, is rock-waste from the surrounding mountains. During an arid period of the early Tertiary the tributaries of the Orange River dried up and became filled with rock-waste and sand transported by wind but mainly by surface water (Villiers and Söhnge 1959).

Soils: The drainage lines and flood plains have rough medium sands with portions of 80 - 90 % medium sand and a stone content of 40 - 60 %. The footslopes and banks have a similar grain composition to the soils of the slopes, silty sand with 39 - 48 % silt. The main salt of both soil types is lime (Tab. 3.3 and 3.4).

Climatic aspects: The flood plains are situated along the dry Orange River valley, where the precipitation is low and the air temperature high. The sea mists do not reach the eastern Gariep, so that the air humidity is low. The drainage system of the silty plains is situated in the western part where the vegetation benefits from precipitation in winter and the air temperature is moderate.

Vegetation pattern and cover: The vegetation forms a regular pattern due to the quickly alternating habitat types of plain surface and drainage lines. Within the silty plains the 'Brownanthus pseudoschlichtianus - Drosanthemum inornatum all.' alternate with the 'Codon royenii - Trichodesma africanum all.' accompanied by many slope species. Whereas the surface of the flood plains is either covered with the 'Prenia tetragonia - Psilocaulon subnodosum ass.' or a scarce meadow of *Stipagrostis obtusa* develops, e.g. in some parts of the Springbokvlakte, or it is devoid of any vegetation. The habitats, which were more often

disturbed by water floods, are covered with the 'Sisyndite spartea - Rogeria longiflora ass.'. In sheltered positions, behind rock outcrops or at the edge of the plains and drainage lines, where silty soil pockets remain, *Brownanthus pseudoschlichtianus* could be observed. The 'Calicorema capitata - Wellstedia dinteri' communities also colonise the banks and footslopes although their soil properties differ from those previously described. The mean ground cover of the flood plains and drainage lines is comparably low with 3 to 17 % (Tab. 3.2). Chamaephytes, phanerophytes and therophytes are represented in equal parts, 34 %, 29 % and 29 % (Fig. 3.8.h). Nearly half of the chamaephytes are leaf succulent (45 %) while stem succulence does not appear.

**Floristic composition:** This vegetation type is characterised by a relatively low mean number of species with 2 - 15 per 100 m<sup>2</sup> (Tab. 3.2). *Codon royenii* (MCh thorny leaf), *Trichodesma africanum* (T/MCh) and *Sesuvium sesuvioides* (T I su) could be observed alongside the channels. *Boscia albitrunca* (P) is a rare but frequent phreatophyte along the drainage lines throughout the whole Richtersveld. Other phreatophytes such as *Euclea pseudebenus*, *Rhus pendulina* and *Schotia afra*, common on the banks of the Orange River, occur frequently in the Eastern Gariep District along the drainage lines.

**Distribution:** The differential species *Codon royenii* and *Trichodesma africanum* are distributed throughout the Nama Karoo, such as *Sesuvium sesuvioides*. But the latter has its distribution centre in the northern part of the Nama Karoo reaching its southern border in the Richtersveld with additional occurrences in the eastern South Africa, the Sudano-Zambesian Region.

## 211 Habitats on gravelly flood plains and drainage lines within the Nama Karoo

Alliance: *Calicorema capitata* - *Wellstedia dinteri* all. prov.

Plots: 5934, 5995, 5999, 6001, 6012, 6163, 6168, 6214, 10017, 10067, 10091, 10096, 10098, 10099, 10103 and 10449

Diagnostic species: *Calicorema capitata*, *Monechma cleomoides* and *Wellstedia dinteri*

The drainage lines and flood plains situated in the east of the Richtersveld show floristic relations to the Nama Karoo plains. *Calicorema capitata* (NP) is, for example, a common element of the broad plains within the Namaland Domain. *Wellstedia dinteri* (MCh) and *Monechma cleomoides* (MCh) have the same distribution area but occur in a lower constancy.

Within the eastern Gariep the slope vegetation shows an obvious differentiation between the upper part of the slope and lower footslope. The lower, gently raising, footslopes show a greater floristic relation to the communities of the flood plains and drainage lines and were therefore joined to the latter.

### 2111 Habitats on the footslopes of the leeward escarpment range

Association: *Euphorbia mauritanica*\_Gariep - *Zygophyllum decumbens* ass. prov.

Plots: 6161, 6164, 6172, 6173, 6178, 6221, 6224, 6226, 6228, 6229, 623, 6232, 6233, 6241, 6242, 10001, 10019, 10022 and 10455

Diagnostic species: *Euphorbia mauritanica*\_Gariep, *Zygophyllum decumbens* and *Cleome semitetranda*

Constant companions: the pioneers *Psilocaulon subnodosum*, *Stipagrostis obtusa* and several therophytes such as: *Enneapogon scaber* and *Cleome foliosa*

Within the contact zone of Nama Karoo and Succulent Karoo (Maerpoort/Rooiberg) the footslopes between 300 and 550 m are characterised by the occurrence of *Euphorbia mauritanica*\_Gariiep (NP s su), *Zygophyllum decumbens* (MCh l su), *Calicorema capitata* and slope species such as *Euphorbia decussata*. *Euphorbia mauritanica*\_Gariiep could also be observed at a higher position on the western slope of the Rooiberg. It has to be mentioned that *Zygophyllum decumbens* is very rare and endemic to the Eastern Gariiep District.

#### 2112 Habitats on the footslopes of the eastern Gariiep mountains

Association: *Calicorema squarrosa* ass. prov.

Plots: 6217, 6256, 6262, 6263, 6292, 6296, 6297, 10004, 10006, 10008, 10010, 10028, 10315 and 10321

Diagnostic species: *Calicorema squarrosa*

On the footslopes of the eastern Gariiep mountains *Calicorema squarrosa* (MCh) and *Calicorema capitata* are combined with the predominating slope vegetation such as *Euphorbia virosa* and mainly *Euphorbia gariepina*, common on gentle slopes. *Calicorema squarrosa* is a rare chamaephyte restricted to the Richtersveld mountains and its surroundings. This association is found between 200 and 500 m elevation for example in the Gannakouriep region.

#### 2113 Habitats on the footslopes of the eastern Gariiep mountains; 100 - 450 m

Association: *Adenolobus garipensis* ass. prov.

Plots: 5996, 5997, 5998, 6002, 6004 6005, 6006, 6014, 10012, 10013, 10016, 10018, 10020 and 10021

Diagnostic species: *Adenolobus garipensis*

Towards the hot Orange River valley *Adenolobus garipensis* climbs up the connected valleys of the eastern Gariiep mountains on the banks of the drainage lines and on footslopes from 100 to 350 m above sea level. The genus *Adenolobus* is common in the Nama Karoo Region.

#### 2114 Habitats on the drainage lines of the eastern Gariiep

Association: *Sisyndite spartea* - *Rogeria longiflora* ass. prov.

Plots: 6003, 6254, 6255, 10092, 10093, 10094, 10095, 10097, 10102, 10308, 10310, 10355, 10394, 10396, 10397, 10414, 10416, 10417, 10418, 10450, 10458 and 10462

Diagnostic species: *Sisyndite spartea*, *Rogeria longiflora* and *Cleome foliosa*

*Sisyndite spartea* (NP rut) and *Rogeria longiflora* (T) are typical species of the Eastern Gariiep District (A. P17). In the Richtersveld they stretch, together with *Calicorema capitata*, along the drainage lines of the eastern Gariiep mountains up to 550 m where *Sisyndite spartea* is replaced by the similar shaped *Monechma spartioides* (NP rut) to the west. The latter is the differential species of the association on drainage lines within the Succulent Karoo characterised by many companions of the Succulent Karoo slopes. *Sisyndite spartea* and *Rogeria longiflora* occur together with *Codon royenii* and *Trichodesma africanum* on the short time habitats directly in the channels,

that are episodically flooded in summer after strong thunderstorms or in winter when large water masses run through the dry scrubland in the eastern Gariep, from the high mountain ranges in the west. The therophyte *Cleome foliosa* is a frequent companion.

### 2115 Habitats on the gravelly flood plains of the eastern Gariep mountains

Association: *Prenia tetragona* - *Psilocaulon subnodosum* ass. prov.

Plots: 5929, 5930, 5931, 5933, 6008, 6009, 6011, 6013, 6015, 6016, 6017, 6251, 10309, 10358, 10362, 10415, 10419, 10433 and 10437

Diagnostic species: *Prenia tetragona*

Constant companions: *Psilocaulon subnodosum*, *Galenia crystallina* and *Hyperthelis salsoloides*

The inner-mountain basins with the 'Brownanthus pseudoschlichtianus - Drosanthemum inornatum' communities are already described in section 1121. Additionally the rare inner-mountain basins of the eastern Gariep have to be mentioned because of another floristic composition. Owing to the high elevation and due to the fact that the granite of the Tatasberg weathered to large rock boulders and rock faces, which give the plain a surplus of water, the kloof is favoured despite its location near to the dry Orange River valley.

Topography: The Kokkerboomkloof (Die Toon) near the Tatasberg and the Springbokvlakte are situated on the same elevation level of 500 m as the Koeroegabvlakte to the west (Fig. 1.2).

The Springbokvlakte descends from 550 - 600 m in the west to 150 m in the east, reaching the level of the Orange River. In the same way the vegetation cover changes (see later).

Soils: The soil properties differ from the habitats of the inner-mountain basins in the west. Within the granite complex of the Tatasberg the grain composition leads to a rough medium sand with 5 % silt and 93 % sand compared to the silty sand of the Koeroegabvlakte with 44 % silt and 54 % sand (Tab. 3.3). Also the portion of stone content is higher (41 % to 8 % in the Koeroegabvlakte). Further downwards (450 m) to the east, the soil type of the Springbokvlakte is a weak silty sand with 20 % silt and 80 % sand (stone content 31 %).

Climatic aspects: Winter rains only rarely reach the inner-mountain basins within the eastern Richtersveld but episodically strong thunderstorms break in during summer.

Vegetation pattern and cover: The vegetation structure of both dwarf shrub formations, 'Prenia tetragona - Psilocaulon subnodosum ass.' and 'Brownanthus pseudoschlichtianus - Drosanthemum inornatum ass.' shows obvious similarities. The ground cover of the former reaches only half of the latter (10 to 17 % mean ground cover), but the distribution of the percentage values is comparable (Tab. 3.2). *Prenia tetragona*, such as *Brownanthus pseudoschlichtianus*, also dominate the association with 5 to 10 %, whereas the other species of the composition share the remaining percentages.

Floristic composition: The upper part of the Springbokvlakte with the Tatasberg pediment and the Kokkerboomkloof are covered with the 'Prenia tetragona - Psilocaulon subnodosum ass.'. *Prenia tetragona* (MCh I su) is accompanied by several pioneers such as *Psilocaulon subnodosum* (NP I su), *Galenia crystallina* (MCh I su) and *Stipagrostis obtusa* (H). The main companion of the 'Brownanthus pseudoschlichtianus - Drosanthemum inornatum all. *Eberlanzia ebracteata\_inland* appears frequently. *Trianthema triquetra*, *Heliophila variabilis*, *Amellus nanus*, *Leysera tenella*, *Gazania lichtensteinii*, *Dimorphotheca sinuata*,

*Acantopsis disperma*, *Ursinia cackilefolia*, *Grielum humifusum* and others make up the ephemeral meadow. *Brownanthus pseudoschlichtianus* could be observed in sheltered positions between rock outcrops, where silty sand remains. The special feature of the Kokkerbomkloof is the name giving species *Aloe dichotoma* (= Kokkerbom). Within the plain *Aloe dichotoma*, coming from the slopes of the 'Ceraria namaquensis - *Aloe dichotoma* all.', forms a sparse Kokkerbom forest under which the *Prekia tetragona* association is represented. Even shoots of the kokkerbom were found.

## 212 Habitats on the gravelly flood plains and drainage lines with additional species of the Succulent Karoo

Alliance: *Stipagrostis namaquensis* all. nov.

Plots: 6000, 10357 and 10443

Diagnostic species: *Stipagrostis namaquensis*

The differential species of the following communities have their distribution centre in the Nama Karoo. But they are characterised by companions of the Succulent Karoo. These are almost species of the slopes that benefit from the surplus of water along the drainage lines. *Stipagrostis namaquensis* is a branched grass (H), which is mainly found in the eastern Gariep.

### 2121 Habitats at elevations of 200 - 450 m

Association: *Leucophris mesocoma* - *Monechma mollissimum* ass. prov.

Plots: 6130, 6134, 6149, 6181, 6182, 6272, 6274, 6275, 6276, 6277, 6279, 6283, 6285, 6286, 6287, 6288, 10055, 10058, 10061 and 10278

Diagnostic species: *Leucophris mesocoma*, *Monechma mollissimum*, *Zygophyllum microphyllum*

In the western Gariep between 200 - 450 m the drainage system is covered by 'Leucophris mesocoma - *Monechma mollissimum* ass.'. *Leucophris mesocoma* (H) is a kneeling grass that forms broad clusters, within which *Monechma mollissimum* (NP) is frequently sprinkled throughout. *Eriocephalus ericoides* (MCh/NP), *Zygophyllum microphyllum* (MCh l su), *Drosanthemum muirii* (MCh l su) and *Prekia sladeniana* (MCh l su), coming from the slopes, are common companions.

Within broad sheet wash valleys small islands of forest are formed by the phreatophyte *Schotia afra* (MiP) with some individuals of *Rhus pendulina* alternating with expanded areas of the 'Leucophris mesocoma - *Monechma mollissimum* ass.'.

### 2122 Habitats at elevations of 450 - 550 m

Association: *Monechma spartioides* - *Cadaba aphylla* ass. prov.

Plots: 10137, 10141, 10143, 10145, 10147, 10152, 10155, 10157, 10161, 10162, 10163, 10166, 10168, 10170, 10171, 10175, 10177, 10184, 10186, 10188, 10190, 10196, 10198, 10291, 10292 and 10293

Diagnostic species: *Monechma spartioides* and *Cadaba aphylla*

The 'Monechma spartioides - *Cadaba aphylla* ass.' occurs at higher altitudes (450-550 m), which can be observed in the Koeroegabvlakte and in the Abiquavvlakte. In the lower parts of the Koeroegab- and Abiquavvlakte, facing the east, the 'Monechma spartioides - *Cadaba aphylla* ass.' changes into the 'Sisyndite spartea - *Rogeria longiflora* ass.' at about 450 m *Monechma spartioides* (NP rut) is widespread in the whole Nama Karoo whereas *Tetragonia reduplicata*

(MCh l su), *Zygophyllum prismatocarpum* (NP l su), *Stipagrostis ciliata* (H), *Lycium ferocissimum* (NP), *Tetragonia reduplicata* (MCh l su), *Nymania capensis* (NPh) and several further species are frequent companions descending from the mountains. As an indicator for lime, *Zygophyllum prismatocarpum* shows the occurrence of lime crust under the silty sand, which can be seen where it is cut by the drainage lines.

### 1131 Habitat on the Orange River terraces

Association: *Brownanthus pubescens* ass. prov.

Plots: 10393, 10395, 10398 and 10400

Diagnostic species: *Brownanthus pubescens*

A special feature can be seen on the lower Pleistocene Orange River terraces in the western Gariiep, the 'Brownanthus pubescens ass.' (see A. T3 and A. T7).

Topography: The terraces are situated at the lower Orange River, where its narrow valley leaves the mountain ranges and extends into a broad plain. Deep incised dry channels subdivide this former riverbed in elongated terraces, which drain into the Orange River.

Geology: The terraces were developed during the Pleistocene when the retreat of the sea caused a further lowering of the coastal area. Rounded pebbles of older rocks, among which quartzite is the most abundant, cover the surface of the terraces, but granites, gneisses, lavas and metamorphic rocks also occur.

Soils: The terraces provide a sandy loam with 14 % clay and 49 % silt (Jähniq 1993). The stone content amounts to 13 % and conductivity reaches high values of up to 9300  $\mu\text{S}/\text{cm}$  (Tab. 3.3, 3.4). The main salts are CaCl, NaCl and gypsum.

Climatic aspects: Situated in front of the escarpment, the terraces rarely receive rain but the influence of the sea mists is high. The low evaluation causes high air temperatures during the day.

Vegetation pattern and cover: The individuals of the low growing *Brownanthus pubescens* (up to 20 cm) form a regular pattern on the surface of the terraces at a distance of about 20 cm to each other. The mean ground cover comes to 15 % (3.2).

Floristic composition and distribution: *Brownanthus pubescens* (MCh l + s su) is only found on these terraces and therefore endemic to the Western Gariiep Circle of the Succulent Karoo Region. This species is frequently accompanied by *Zygophyllum patenticaule* (MCh l su) and *Cheiridopsis robusta* (MCh l su), which are able to cope with high amounts of gypsum. *Trianthema triquetra* (T) and other therophytes are commonly observed.

This association is highly endangered because the terraces are extensively mined and secondly the slag from the mines is being continuously deposited onto the terraces and plains further inland (Foto. A. P20).

### 3211 Species of edaphically salt habitats on ravines

Community: *Tamarix usneoides* - *Cyperus marginatus*

Only salt resistant species are able to survive where water basins are formed within the drainage system. *Tamarix usneoides* (MiP), *Cyperus marginatus* (H) and a grass, Gramineae 109552, are often observed on these edaphic salt habitats. A rare and newly described species, *Limonium dyeri* (MCh) is sprinkled in amongst the broad grass clusters.

### 3212 Open sand plains

Community: *Stipagrostis obtusa* com.

Both plains, the Springbokvlakte and the Annisvlakte are almost void of any vegetation cover. The reason for this can be found in different circumstances. The lower part of the Springbokvlakte is situated in direct contact to the hot Orange River valley, at 150 m altitude and therefore in a rain shelter with hot air temperatures (A. P18). Only the pioneer *Stipagrostis ciliata* is able to resist these conditions with a low density 0.01 % per 100 m<sup>2</sup> with some therophytes such as *Trianthena triquetra*, *Dicoma capensis* and *Mesembryanthemum gariusanum*. A small strip of the upper Springbokvlakte is covered by the 'Brownanthus pseudoschlichtianus - Drosanthemum inornatum all.'. The conditions of the habitats on the lower Annisvlakte are probably similar. It also lies at a low elevation of 200 to 300 m and the distance to the lower Orange River valley is not that far, so that air temperature is high and precipitation in front of the escarpment low. Due to this fact, the lower Annisvlakte is also covered with a scarce meadow of *Stipagrostis obtusa*. In contrast to the Springbokvlakte the upper part of the Annisvlakte, where habitat conditions near the escarpment are more favourable, a vegetation cover is still almost absent. *Euphorbia gummifera* is the only remaining unpalatable shrub accompanied by *Stipagrostis obtusa* and several indicators for disturbance such as *Opophytum aquosum* or *Mesembryanthemum squamulosum* were observed. It is suggested that in former times the upper plain was also covered by the 'Brownanthus pseudoschlichtianus - Drosanthemum inornatum' community but was successively over grazed. Khubus, the main village in this region is situated on the southern footslope of the Goariëp mountains. The Annisvlakte may have served as favourable pasture for the herds of the inhabitants of Khubus. The remaining *Euphorbia gummifera* could be seen as a relic of the former Brownanthus pseudoschlichtianus - Drosanthemum inornatum community on the Annisvlakte indicating the mentioned hypothesis. On the inner-mountain plains *Euphorbia gummifera* also occurs within the 'Brownanthus pseudoschlichtianus - Drosanthemum inornatum' community along the footslope.

Both plains were not investigated because of their low vegetation cover density, so that a classification of this community is absent.

### 3111 Species of the gallery forest along the Orange River banks

Community: *Rhus pendulina* - *Ziziphus mucronata*

An azonal vegetation type is gathered along the Orange River valley (A. P12). The dominant phreatophytes of the gallery forest along the Orange River banks are *Rhus pendulina* and *Ziziphus mucronata*. *Rhus pendulina*, *Tamarix usneoides*, *Euclea pseudebenus*, *Maytenus linearis*, *Ricinus communis*, *Prosopis glandulosa* and *Acacia karoo* are frequently intermingled. The species are widespread especially in the western part of southern Africa; only *Rhus pendulina* is restricted to the Orange River valley.

### 3 Special habitats (Pioneers, Ruderals, Phreatophytes)

Several species do not follow the large spatial changing climate gradient from the coast inland but profit from their wide ecological amplitude. They are able to colonise newly established or extreme habitats.

Pioneers such as e.g. *Galenia crystallina* (MCh I su) and *Psilocaulon subnodosum* (NP I su) are observed on sandy and gravel surfaces of riverbeds, runnels and flood plains in the whole

mountain region and the coastal plain. Typical sites are also detritus of high mountains. They withstand rubble over runs and surface movements. With *Codon royenii*, *Trichodesma africanum*, *Monechma spartioides*, *Sisymbrium sparteum* and others they populate the drainage lines all over the mountainous Richtersveld. Other typical habitats for these pioneers are the flood plains in the east (Maerpoortvlakte), where water floods brought surfaces after exceptional and intense summer thunderstorms. Both, *Galenia crystallina* and *Psilocaulon subnodosum* are leaf succulent chamaephytes and have their main distribution in the Succulent Karoo Region (Jürgens 1991, Klak & Linder 1998). Due to their competitive incidence on sandy gravel sites where the groundwater-table is periodically high they are not restricted to the more humid Succulent Karoo, but also colonise the flood plains and runnels in the more arid Eastern Gariep District of the Nama Karoo Region.

On disturbed or grazed sites, such as on the plains or on footslopes where the grazing intensity is high, they are combined with grazing indicators such as *Mesembryanthemum squamulosum* (T l su), *Mesembryanthemum hyperthropicum* (T l su), *Psilocaulon salicornioides* (MCh s + l su) and others.

The common species *Hyperthelid salsoloides* (MiCh l su) is widespread throughout South Africa and southern Namibia with its focus in the Richtersveld (32% constancy) .

### 3.2. Ordination

Several environmental factors were ascertained in order to understand the environmental control of spatial vegetation patterns, species composition, diversity and distribution. The regional influence of the climate is shown by the factors air temperature, precipitation and cloudiness. The local influence of the relief is expressed by altitude, exposition and inclination. The physical and chemical soil properties characterise the habitat surface. The high diverse geology of the Richtersveld also possibly influences the vegetation distribution. The geological units according to Villiers & Söhnge (1959) are assigned to the sites. The habitat features of the vegetation communities have already been described in the previous chapter. The ordination analyses should give an insight into the main determining factors and their significant influence on the vegetation.

Initially the main factors that determine the regional distribution of the five basic groups were analysed, and secondly the five groups were investigated separately.

#### 3.2.1. Data set of all 230 classified relevés

##### *Spearman's rank correlation coefficient*

In total 26 environmental variables were available for the total data set. Though it can be assumed that several of these variables are correlated amongst each other. To find correlating variables the Spearman's rank correlation coefficient was calculated shown in the correlation matrix (A. 4). Several climatic variables have strong correlations among each other. For the ordination analyses it is important to choose the most explanatory variables which best represent the omitted correlating variables. Appendix A. 3 shows



a scatterplot matrix for the climatic variables in which each variable is plotted against each other. The precipitation total during winter follows the altitudinal gradient. The coastal plain rarely receives any rain, but the precipitation increases rapidly with the ascent into the Vandersterrberg - Stinkfonteinberge. On the leeward side, to the east, the precipitation value again decreases continuously. This variable is only negatively correlated to the mean air temperature and the sunshine duration in summer. The mean monthly maximum air temperature during the summer clearly represents the coast-inland gradient along which the temperature increases from the coast into the interior. This variable is positively correlated to the summer climatic variables, sunshine duration, rainy days, mean monthly air temperature, air temperature range, mean monthly minimum air temperature and to the winter air temperature range. It is negatively correlated to the winter climatic variables, rainy days and mean monthly minimum air temperature, but it is not correlated to the winter precipitation. Therefore the winter precipitation total and the mean monthly maximum air temperature are the two non-correlated climatic variables which best represent the regional influence of the climate.

The geological unit 'G00' stands for Quaternary sediments and is highly correlated with the soil textures silty medium sand and sandy silt. It joins the soil textures silty fine sand, medium sand and silty medium sand and could therefore be eliminated. The sandy silt is correlated with the geological unit 'G08' because the gray gneissic granite of the Violdsdrif Suite is only covered by sandy silt. So it could be omitted.

The medium sand correlates with the mean monthly maximum air temperature in summer. It is assumed that the regional distribution of the vegetation mainly depends on climatic factors. So the medium sand was omitted from further analyses.

#### *Forward Selection*

The eleven remaining variables were entered into the Forward Selection module of CANOCO to reduce them to the most explanatory factors (A. 4). Seven variables show high significance ( $p \leq 0.005$ ). Mainly the geological units (G04, G05, G06 and G09 see abbreviations A. 1) were shown to be weak explanatory factors and were therefore omitted from further ordination analyses. The climatic variables, mean monthly maximum air temperature in summer and precipitation total in winter, the soil variables, silty fine sand, silty medium sand and sandy silt and the geological units 'G02' (medium-grained non-porphyrific granite of the Tatasberg Complex) and 'G11' (quartzite and sandstone of the Stinkfontein Formation) were the remaining variables, which were entered into the ordination analyses.

#### *Canonical Correspondence Analysis (CCA)*

The results of the ordination with the canonical correspondence analysis of the total data set are shown in Fig. 3.11. The eigenvalues for axis 1 and axis 2 are quite high with 0.65 and 0.41 and show strong gradients (Tab. A.4). The Monte Carlo test for the

species-environment correlation underlines the strong correlation of the species to the environmental factors. The first axis reaches 0.94, the second axis 0.85 and the third axis 0.78 (Tab. A .4).

Axis one reflects the regional climatic gradient. The winter precipitation total is low at the coast (left side), increases rapidly at the escarpment (middle) and decreases considerably leeward of the eastern Gariep (right side). In contrast the mean monthly maximum air temperature in summer is low at the coast and increases into the interior. In consequence the sandy habitats of the coastal plain with the 'Eberlanzia ebracteata\_coast - Lebeckia multiflora all.' is situated on the left hand side, the Nama Karoo slope habitats and the habitats of the flood plains and drainage lines with the 'Ceraria namaquensis - Aloe dichotoma all.' and the 'Calicorema capitata - Wellstedia dinteri all.' lie to the right. The middle position is represented by the slope habitats and silty plain habitats of the Succulent Karoo with the 'Tylecodon paniculatus - Osteospermum armatum sub-ord.' and the 'Brownanthus pseudoschlichtianus - Drosanthemum inornatum all.'.

The second axis separates the plain habitats from the slope habitats mainly by the variables sandy silt, silty fine sand and silty medium sand respectively.

#### *Detrended Correspondence Analysis (DCA) and Principle Component Analysis (PCA)*

These two indirect ordination analyses should serve as independent comparisons. In contrast to the CCA both ordination methods are first performed on the species data alone, and then the environmental data are superimposed onto the ordination plots.

The results of both, PCA and DCA (Fig. 3.12 and Fig. 3.13) are similar to the CCA. The main groups are separated along the same axis of the CCA. Only the separation of the groups is not as clear. The eigenvalues of the PCA also reach high values for axis 1: 57.66 % and axis 2: 35.77 % (cross-products matrix is variance-covariance centred by species) and explain over 90 % of the data set. The DCA and PCA diagrams show an almost similar distribution and separation of the vegetation communities, which underlines the correctness of the CCA.

### **3.2.2. Data set of 251 relevés with soil properties only**

The pH-value, electrical conductivity, carbonate content, soil texture, soil colour, and stone content were investigated for 251 relevés to examine the influence of the soil properties on the vegetation (A. 13, A. 14).

The carbonate content correlates positively with the pH-value and was therefore eliminated from further analyses (A .5). The fine substrate fraction correlates negatively with the gravel fraction and positively with the medium sand and was also omitted. The two gravel fractions correlate positively with each other hence the coarse gravel was eliminated.

The remaining variables, fine gravel content, silty fine sand, sandy silt, silty medium sand, pH-value and electrical conductivity show a high significance ( $p \leq 0.005$ ) within

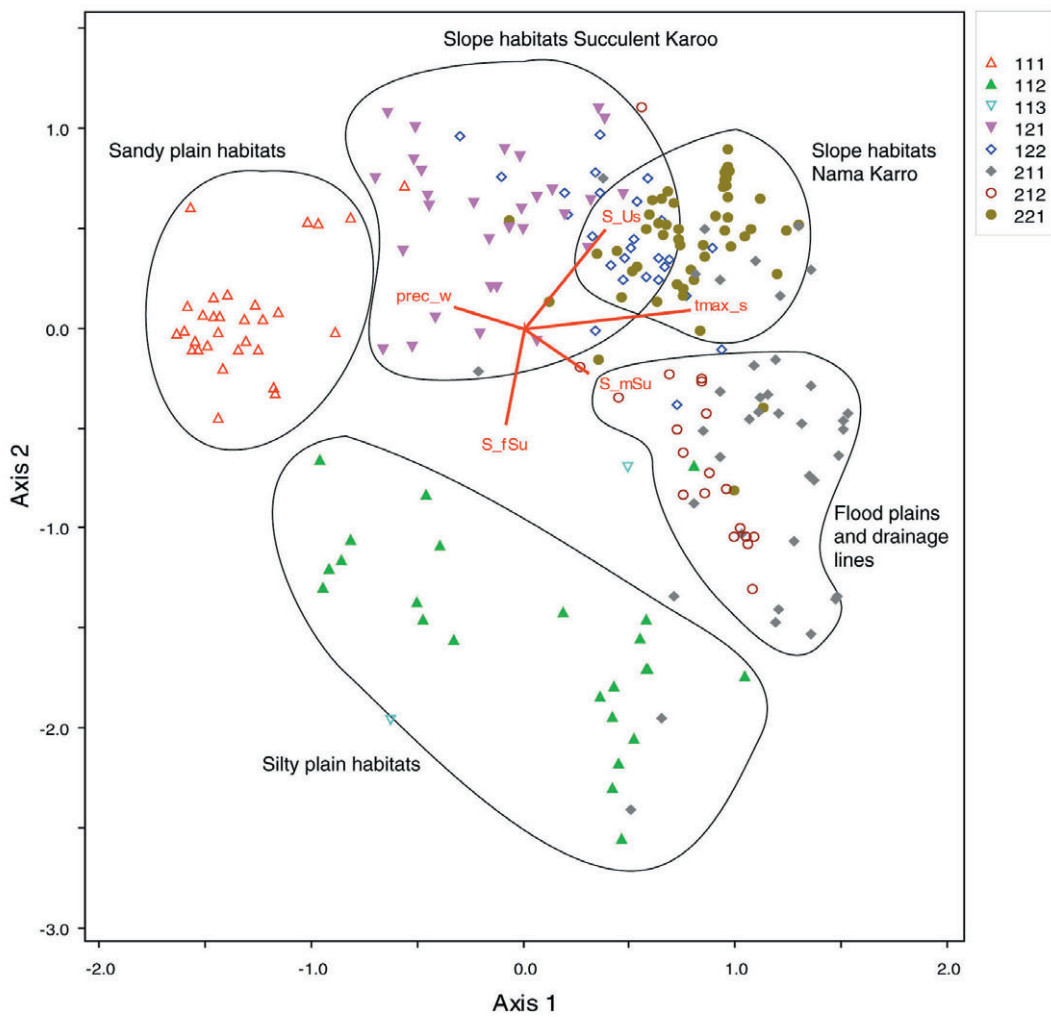


Fig. 3.11: Biplot of the Canonical Correspondence Analysis (CCA) for the data set of all 230 classified relevés. The number in the legend is the numerical code of the syntaxa: 111 = *Eberlanzia ebracteata* coast - *Lebeckia multiflora* all.; 112 = *Brownanthus pseudoschlichtianus* - *Drosantheum inornatum* all.; 113 = *Brownanthus pubescens* ass.; 121 = *Didelta spinosa* - *Helichrysum hebelepis* all.; 122 = *Chrysocoma puberula* - *Menodora juncea* all.; 211 = *Calicorema capitata* - *Wellstedia dinteri* all.; 212 = *Stipagrostis namaquensis* all.; 221 *Ceraria namaquensis* - *Aloe dichotoma* all. The ordinations are based on species cover and 7 environmental variables. *Prec\_w* = average monthly precipitation total in winter; *tmax\_s* = average monthly air temperature in summer; *S\_Us* = soil texture sandy silt; *S\_mSu* = soil texture silty medium sand and *S\_fSu* = soil texture silty fine sand. The length of the arrow shows the importance of the environmental variable for the vegetation.

the Forward Selection analysis (A .5), so that they were all entered into the CCA. The importance of the variables decreases from the fine gravel content with  $F \leq 9.7$  to the electrical conductivity with  $F \leq 1.87$ .

The eigenvalues of axes 1, 2 and 3 are 0.54, 0.36 and 0.26; the sum of all canonical eigenvalues comes to 1.44 (Tab. A .5). This means, that the first axis explains 38 %

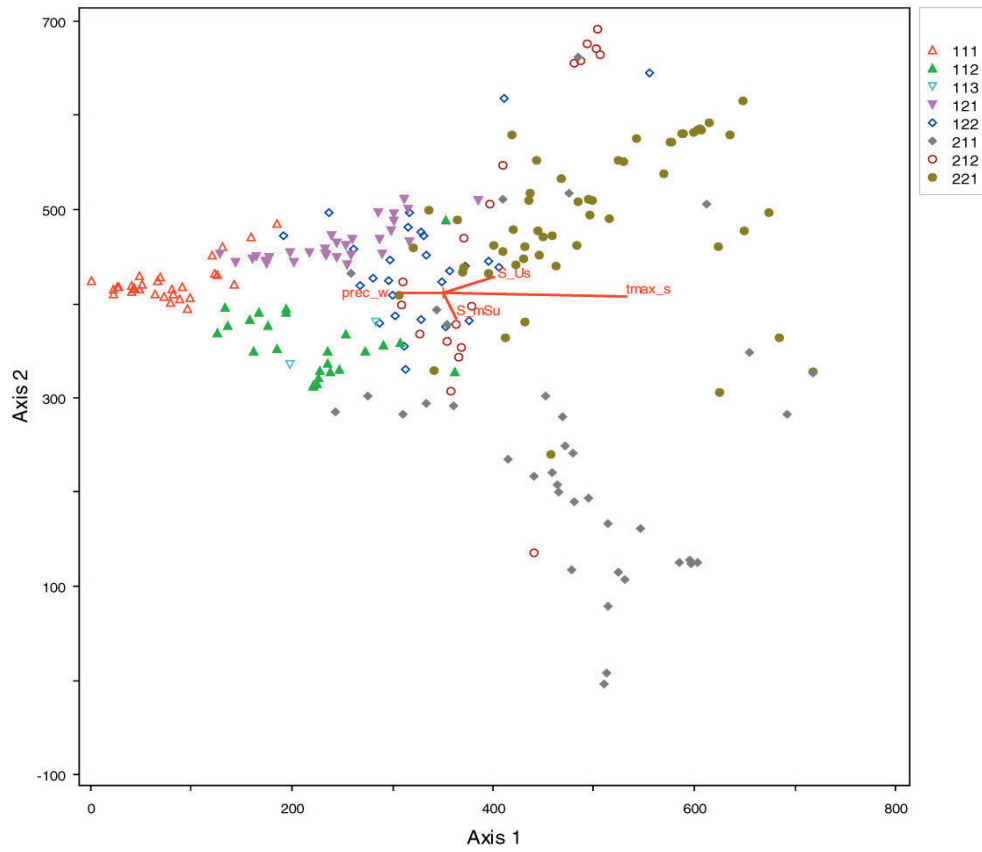


Fig. 3.12: Joint plot of the Principal Components Analysis (PCA) of all 230 classified relevés. Numerical code and environmental variables as in Fig. 3.11.

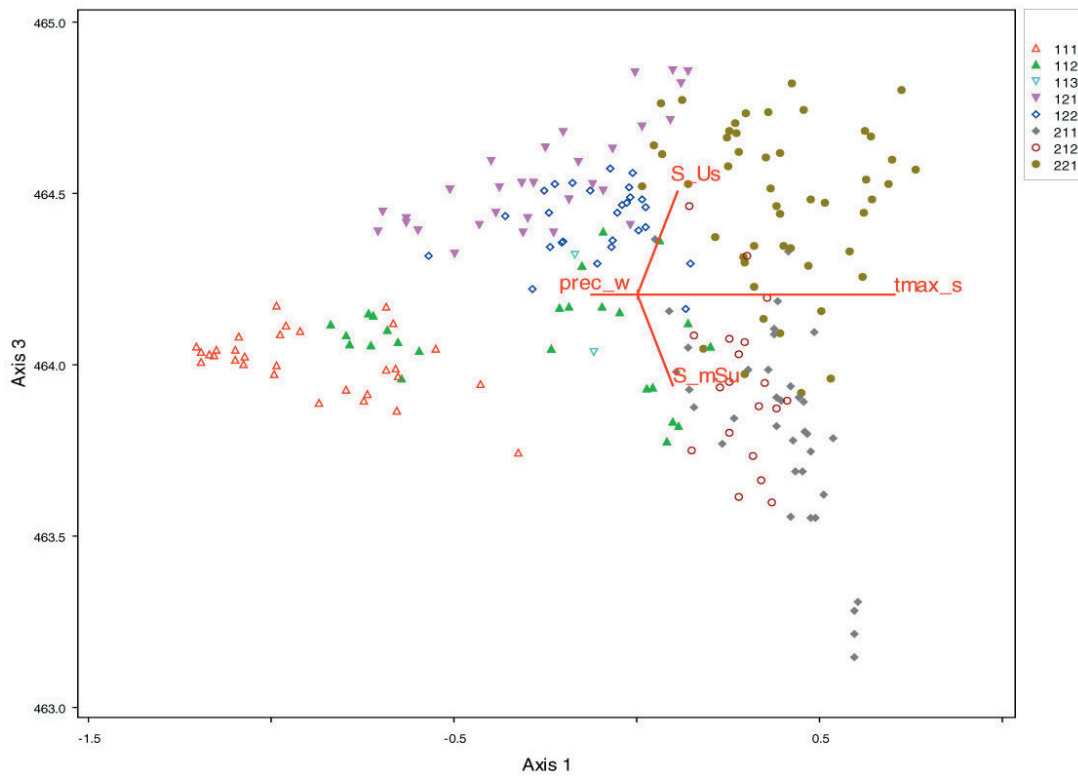


Fig. 3.13: Joint plot of the Detrended Correspondence Analysis (DCA) of all 230 classified relevés. Numerical code and environmental variables as in Fig. 3.11.

of the total variance of the data set, the second 25 % and the third 18 %. The first three axes account for 81 % altogether.

The first axis separates the sandy habitats of the coastal plain without any stone content from the other habitats, in which the Nama Karoo slope habitats and the habitats of flood plains and drainage lines have the most fine gravel content (Fig. 3.14). The silty plains are situated in a central position.

The second axis shows the pH-gradient of the first 10 cm of soil. The pH-value correlates with the carbonate content which reaches its highest values in the soils of the silty plains. The habitats of the flood plains and drainage lines show lower pH-values, followed by the Nama Karoo slopes. The Succulent Karoo slope habitats and even more the sandy habitats of the Sandveld have the lowest pH-values.

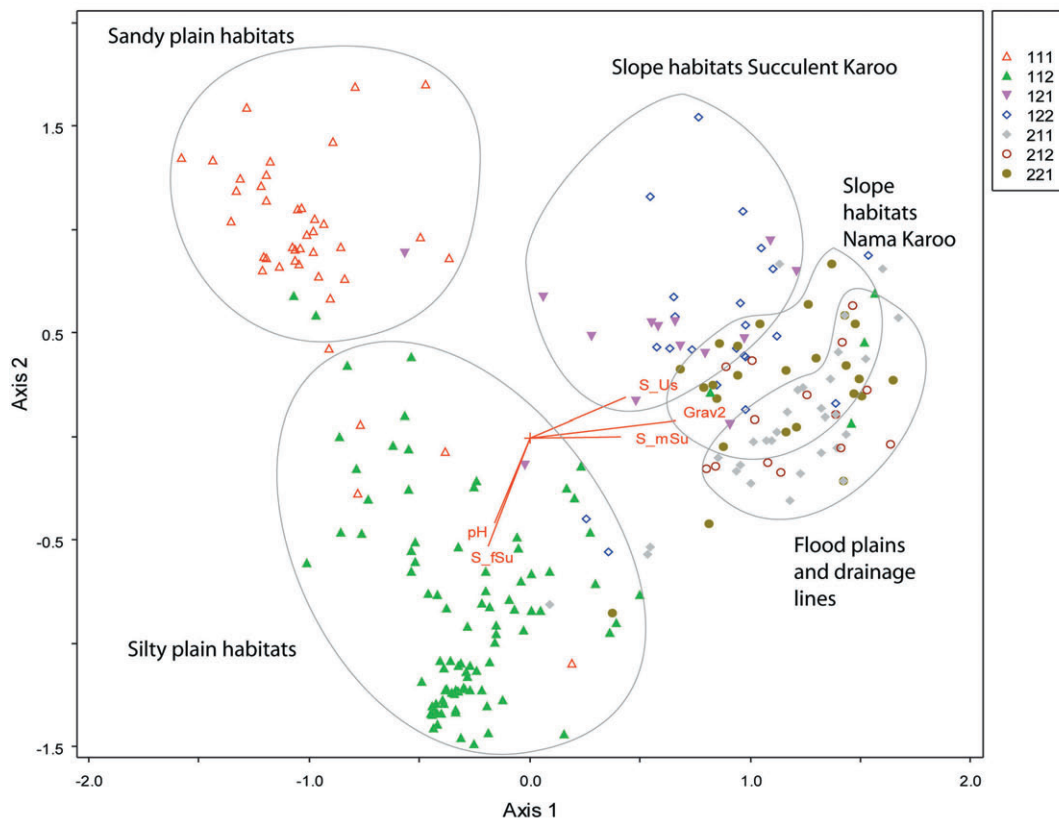


Fig. 3.14: Biplot of the CCA for the data set of all 251 relevés with soil properties only, axis 1 and 2. The number in the legend is the numerical code of the syntaxa: 111 = *Eberlanzia ebracteata*\_coast - *Lebeckia multiflora* all.; 112 = *Brownanthus pseudoschlichtianus* - *Drosanthemum inornatum* all.; 113 = *Brownanthus pubescens* ass.; 121 = *Didelta spinosa* - *Helichrysum hebelepis* all.; 122 = *Chrysocoma puberula* - *Menodora juncea* all.; 211 = *Calicorema capitata* - *Wellstedia dinteri* all.; 212 = *Stipagrostis namaquensis* all.; 221 *Ceraria namaquensis* - *Aloe dichotoma* all. The CCA is based on species cover and 6 environmental variables. PH = pH-value of the first 10 cm soil; Grav2 = fine gravel; S\_Us = soil texture sandy silt; S\_mSu = soil texture silty medium sand and S\_fSu = soil texture silty fine sand.

The third axis divides the sandy habitats (Sandveld) from the silty habitats (all slope sites), silty medium sand habitats (flood plains and drainage lines) and from the silty fine sand habitats (silty plains of the coastal plain and inner-mountain basins, Fig. 3.15). The electrical conductivity is not strong enough within the CCA to explain the variation of the data set.

The separation of the vegetation units is not as clear as in the CCA with all the climatic, geological and relief variables because the relevés with soil samples are not all classified. That means vegetation plots with transition position are also present in the analysis, which covers the unit borders.

### 3.2.3. Data set of 251 relevés with all environmental variables

The CCA with soil properties and all other variables was run, to prove the importance of the soil properties, due to vegetation patterns and species composition. The result of the CCA is more or less similar to the CCA with soil properties only. The diagram of the former shows a clearer grouping of the vegetation units (Fig. 3.16) but the distribution of the plots is almost the same. The fine gravel content correlates positively with the mean monthly maximum air temperature in winter and negatively with the medium

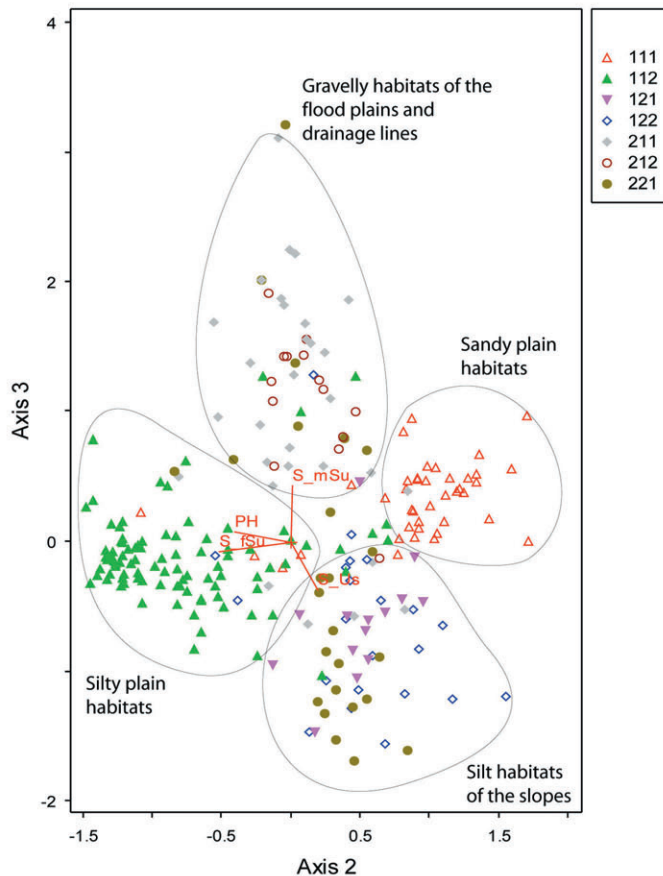


Fig. 3.15: Biplot of the CCA for the data set of all 251 relevés with soil properties only, axis 2 and 3. Numerical code and environmental variables as in Fig. 3.14.

sand soil texture (A .6). The medium sand would therefore extend parallel to the mean air temperature in winter, which is also correlated with the mean monthly maximum air temperature in winter. The sandy silt soil texture correlates positively with the inclination, which is reasonable owing to the fact that all inclined slope habitats have sandy silt soils. The inclination therefore separates the plain from the slope habitats.

The high significant variables ( $p \leq 0.005$ ), which entered the CCA, are the following with decreasing importance (A .6): fine gravel content, mean air temperature in winter, sandy silt soil texture, silty medium sand, precipitation total in winter, pH-value, silty medium sand, soil texture and the geological variable 'G08' (gray gneissic granite of the Vioolsdrif Suite). The sum of all canonical eigenvalues reached 2.23 divided into 0.58 of axis one, 0.46 of axis two and 0.29 of axis three. The first three axis explain

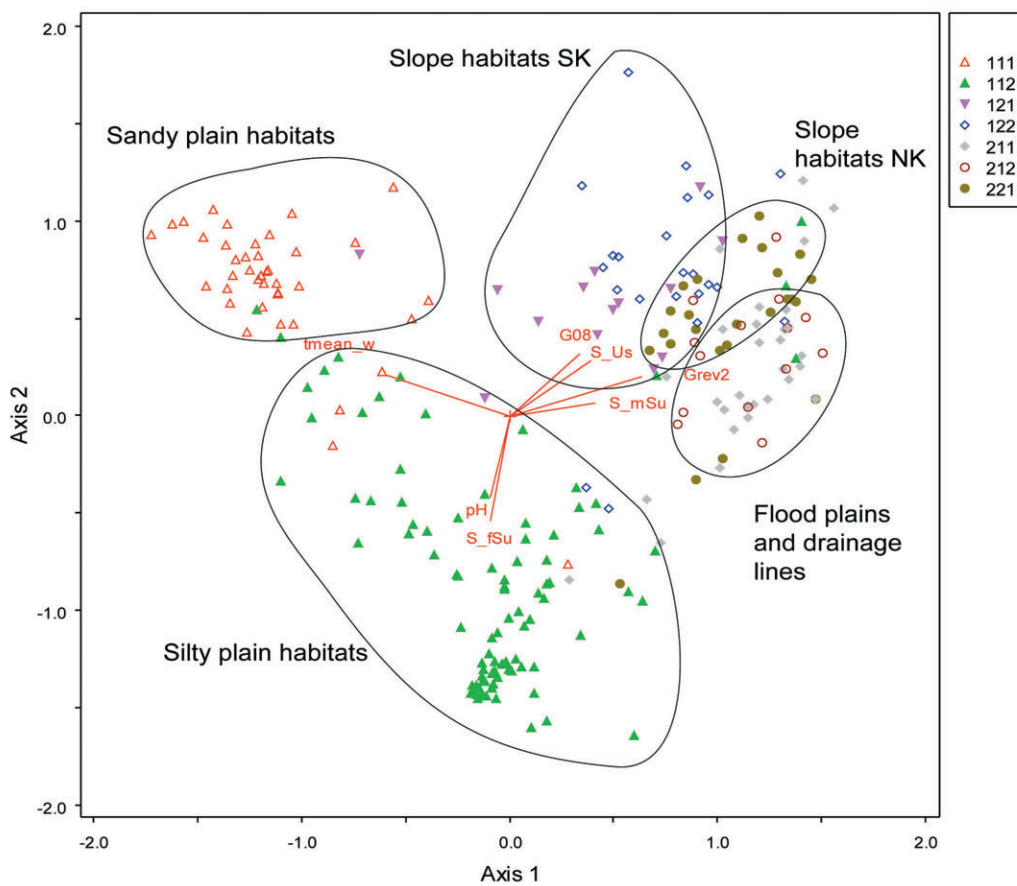


Fig. 3.16: Biplot of the CCA for the data set of all 251 relevés with all environmental variables. The number in the legend is the numerical code of the syntaxa: 111 = *Eberlanzia ebracteata*\_coast - *Lebeckia multiflora* all.; 112 = *Brownanthus pseudoschlichtianus* - *Drosanthemum inornatum* all.; 113 = *Brownanthus pubescens* ass.; 121 = *Didelta spinosa* - *Helichrysum hebelepis* all.; 122 = *Chrysocoma puberula* - *Menodora juncea* all.; 211 = *Calicorema capitata* - *Wellstedia dinteri* all.; 212 = *Stipagrostis namaquensis* all.; 221 *Ceraria namaquensis* - *Aloe dichotoma* all. The CCA is based on species cover and 8 environmental variables. *tmean\_w* = average monthly air temperature in winter; *G08* = gray gneissic-granite of the Vioolsdrif Suite ; *pH* = pH-value of the first 10 cm soil; *Grav2* = fine gravel; *S\_Us* = soil texture sandy silt; *S\_mSu* = soil texture silty medium sand and *S\_fSu* = soil texture silty fine sand.

59.4 % of the total data set variance, 26 % are explained by the first axis, 20.5 % by the second and only 12.9 % by the third axis (Tab. A. 6).

Like in the other CCA with soil properties only the first axis separates the more temperate habitats of the coastal plain from the more arid habitats of the Nama Karoo slopes and flood plains and drainage lines. The strong relationship between the silty fine sand habitats and high pH-values, which is positively correlated with the carbonate content is obvious in both CCAs with physical and chemical soil properties. The sequence of the soil texture along the pH-gradient, which stretches parallel to axis two, is as follows: The highest values are found in the silty fine sand soils, followed by the silty medium sand soils. The sandy silts of the slope habitats and the sandy soils of the Sandveld have the lowest pH-values.

The climate factors explain the first axis and control the distribution of the vegetation on a regional scale. Whereas the importance of the factor soil reveal more on a local scale (see below, section 3.2.4).

### 3.2.4 Data set of the coastal plain habitats

The recorded variables for the coastal plain are highly correlated amongst each other (A .7). The only remaining variables are the air temperature range in winter and the silty fine sand soil texture. Both are significant and entered the CCA (A .7).

The sum of all canonical eigenvalues comes to 1.2. The eigenvalues of the first three axis are 0.7, 0.52 and 0.54. The first two axis explain 100 % of the species - environment relation within the data set. The first axis already explains 56 % (Tab. A .7).

The first axis is correlated with the soil texture, which separates the 'Cheiridopsis robusta - Ruschia leucosperma ass.' of the 'Brownanthus pseudoschlichtianus - Drosanthemum inornatum all.' on silty fine sand habitats further inland, from the communities of the sandy habitats along the coast (Fig. 3.17). The second axis follows the gradient of the air temperature range in winter which splits of the 'Zygophyllum clavatum - Euphorbia brachiata ass.' at the coastline on white sand from the syntaxa of the 'Zygophyllum morgsana - Hermannia trifurca ass.' further inland on red sand. Moving inland the 'Jordaniella clavifolia - Chaetobromus involucreatus sub-ass.', then the 'Brownanthus arenosus sub-ass.' and lastly the 'Cladoraphis spinosa - Limeum fenestratum v. fenestratum sub-ass.' occur on the red dune where the air temperature range in winter receives the highest values on the coastal plain. The air temperature range in winter correlates positively with the sunshine duration. That means, at the coast where the sunshine duration is low the temperature range is also low and further inland with increasing sunshine duration the temperature range increases as well. This phenomenon is caused by the sea mists, which drive inland from the sea where they disperse.

The PCA diagram (Fig. 3.18) shows an almost similar distribution and separation of the vegetation communities, which underlines the accuracy of the CCA.



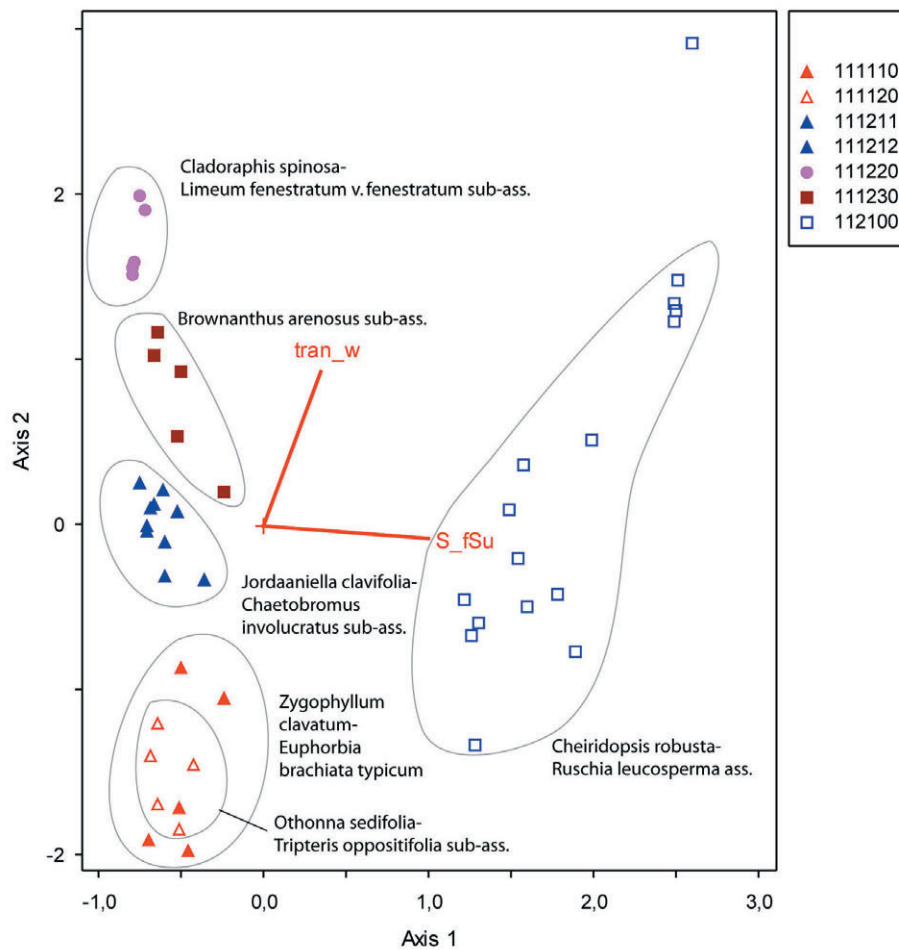


Fig. 3.17: Biplot of the CCA for the habitats on the coastal plains. The number in the legend is the numerical code of the syntaxa: 11111 = *Zygophyllum clavatum* - *Euphorbia brachiata* typicum; 11112 = *Othonna sedifolia* - *Tripteris oppositifolia* sub-ass.; 111211 = *Jordaniella cuprea* - *Crassula atropurpurea* v. *cultriformis* var.; 111212 = *Stoeberia utilis* - *Ruschia Sarmetosa* ascending fruits var.; 11122 = *Cladoraphis spinosa* - *Limeum fenestratum* v. *fenestratum* sub-ass.; 111230 = *Brownanthus arenosus* sub-ass.; 1121 = *Cheiridopsis robusta* - *Ruschia leucosperma* ass. The CCA is based on species cover and two environmental variables. *Tran\_w* = average monthly air temperature range in winter and *S\_fSu* = soil texture silty fine sand.

### 3.2.5 Data set of the slope habitats

The climatic factors, total winter precipitation and mean monthly maximum air temperature are also the most suitable for the slope habitats (A. 8). Forward Selection of the CANOCO module reveals eight non-correlating variables as significant with  $p \leq 0.005$  (A. 8). The most important variables are the mean monthly maximum air temperature,

the geological variable 'G02' (medium-grained non-porphyrific granite of the Tatasberg Complex) and the exposition (N-S). Also significant are 'G09' (ultrametamorphosed sediment of the Violsdrif Suite), the inclination, 'G08' (gray gneissic granite of the Violsdrif Suite) and 'G04' (light coloured schist of the Orange River Group). Axis one separates the Succulent Karoo slopes from the Nama Karoo slopes along the climatic gradient of total winter precipitation, decreasing from west to east, and mean monthly maximum air temperature, increasing from west to the east explaining 28 % of the species-environment relationship (Tab. A. 8, Fig. 3.19, 3.20). Along the second axis, which explains 20 %, the communities of the south exposed slopes of the Koeroegab and Numees mountains are split from the communities of more northerly exposed slopes such as in the hot eastern Gariiep with 'Euphorbia virosa - Euphorbia gariepina ass.'.

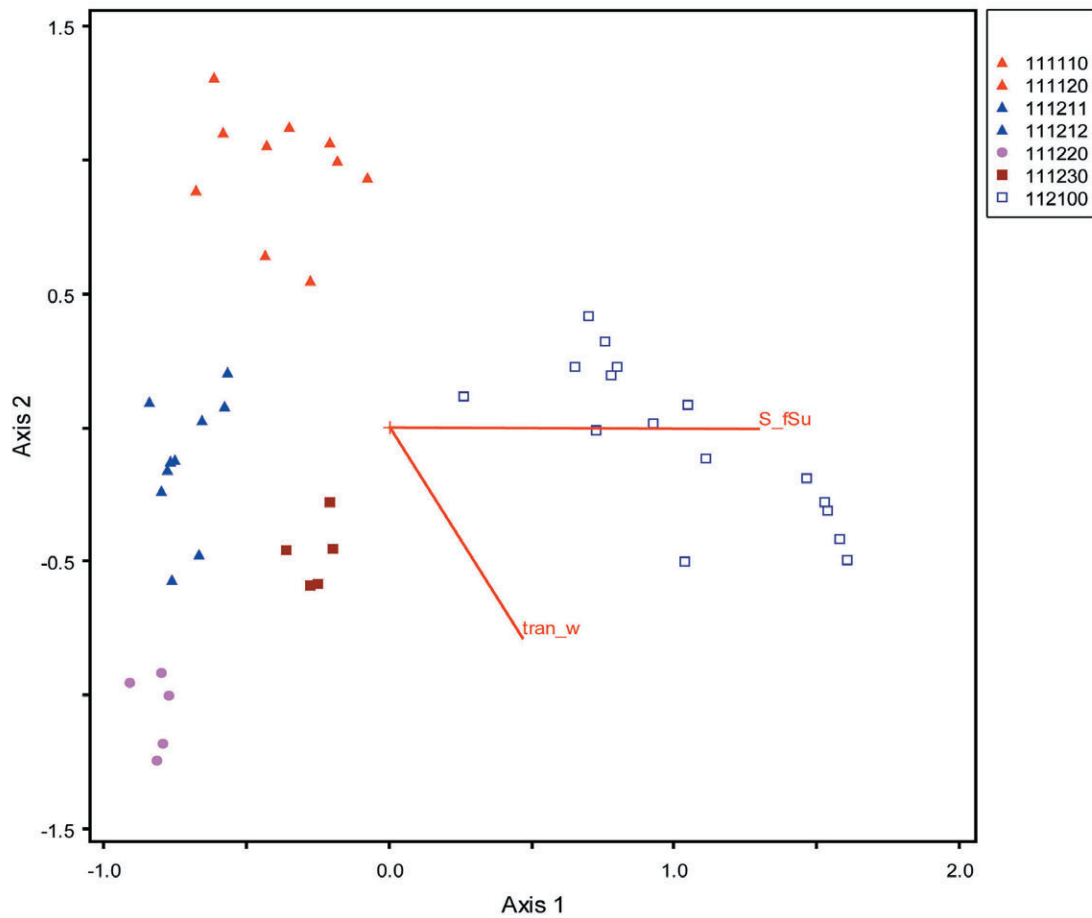


Fig. 3.18: Joint plot of the Principal Components Analysis (PCA) for the habitats on the coastal plains. Numerical code and environmental variables as in Fig. 3.17.

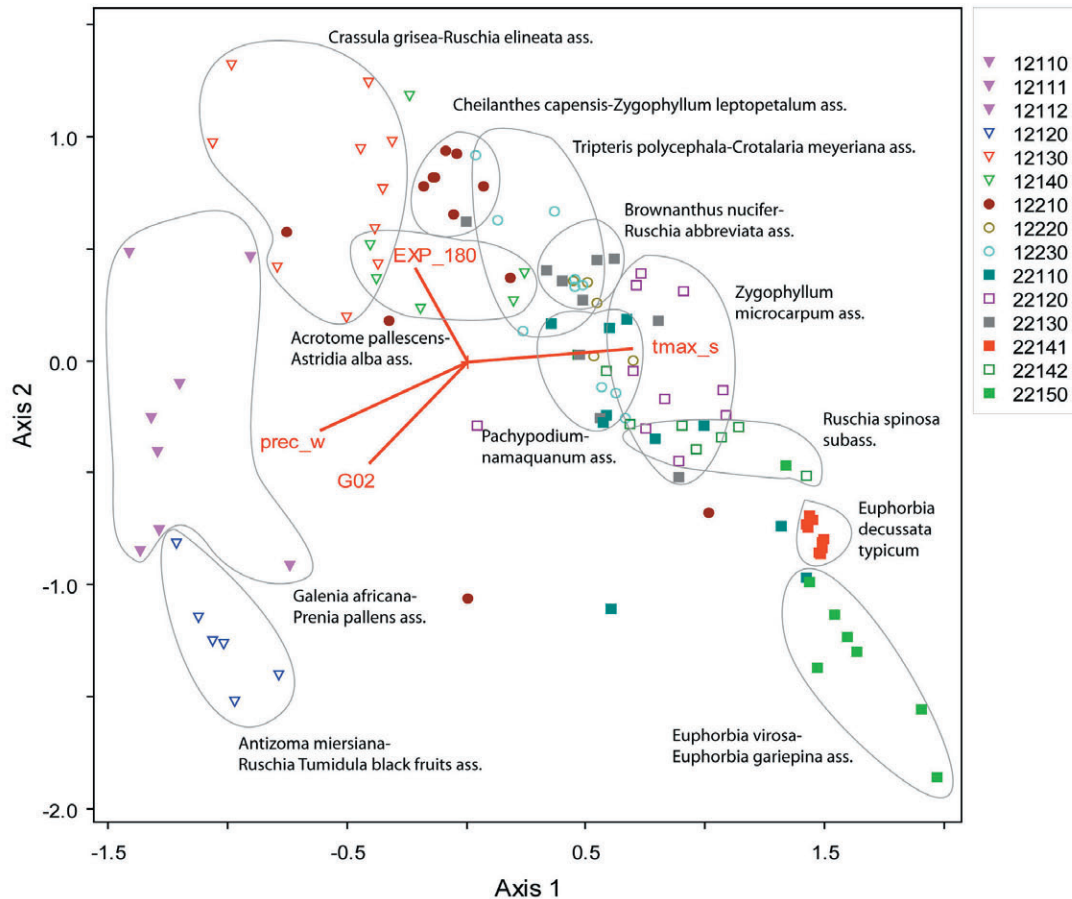


Fig. 3.19: Biplot of the CCA for the slope habitats of the Richtersveld mountain region, axis 1 and 2. The number in the legend is the numerical code of the syntaxa: 1211 = *Galenia africana* - *Prenia pallens* ass.; 12111 = *Elytropappus rhinocerotis* - *Merxmüllera dura* sub-ass.; 12112 = *Pteronia divaricata* - *Berkheya canescens* sub-ass.; 1212 = *Antizoma miersiana* - *Ruschia Tumidula\_black fruits* ass.; 1213 = *Crassula grisea* - *Ruschia elineata* ass.; 1214 = *Acrotome pallescens* - *Astridia alba* ass.; 1221 = *Cheilanthes capensis* - *Zygophyllum leptopetalum* ass.; 1222 = *Ruschia brevibracteata* - *Lycium hirsutum* ass.; 1223 = *Tripteris polycephala* - *Crotalaria meyeriana* ass.; 2211 = *Pachypodium namaquanum* ass.; 2212 = *Zygophyllum microcarpum* ass.; 2213 = *Brownanthus nucifer* - *Ruschia abbreviata* ass.; 22141 = *Euphorbia decussata typicum*; 22142 = *Ruschia spinosa* sub-ass.; 2215 = *Euphorbia virosa* - *Euphorbia gariepina* ass. The CCA is based on species cover and eight environmental variables. *Prec\_w* = average monthly precipitation total in winter; *tmax\_s* = average monthly maximum air temperature in summer; *EXP\_180* = north-south exposition, *G02* = medium-grained non-porphyrific granite of the Tatasberg Complex.

The third axis, explaining only 12 %, is mainly determined by the inclination, which separates the vegetation units of the steep slopes such as in the Koeroegab mountains from the units of gentle slopes e.g. in the Numees mountains.

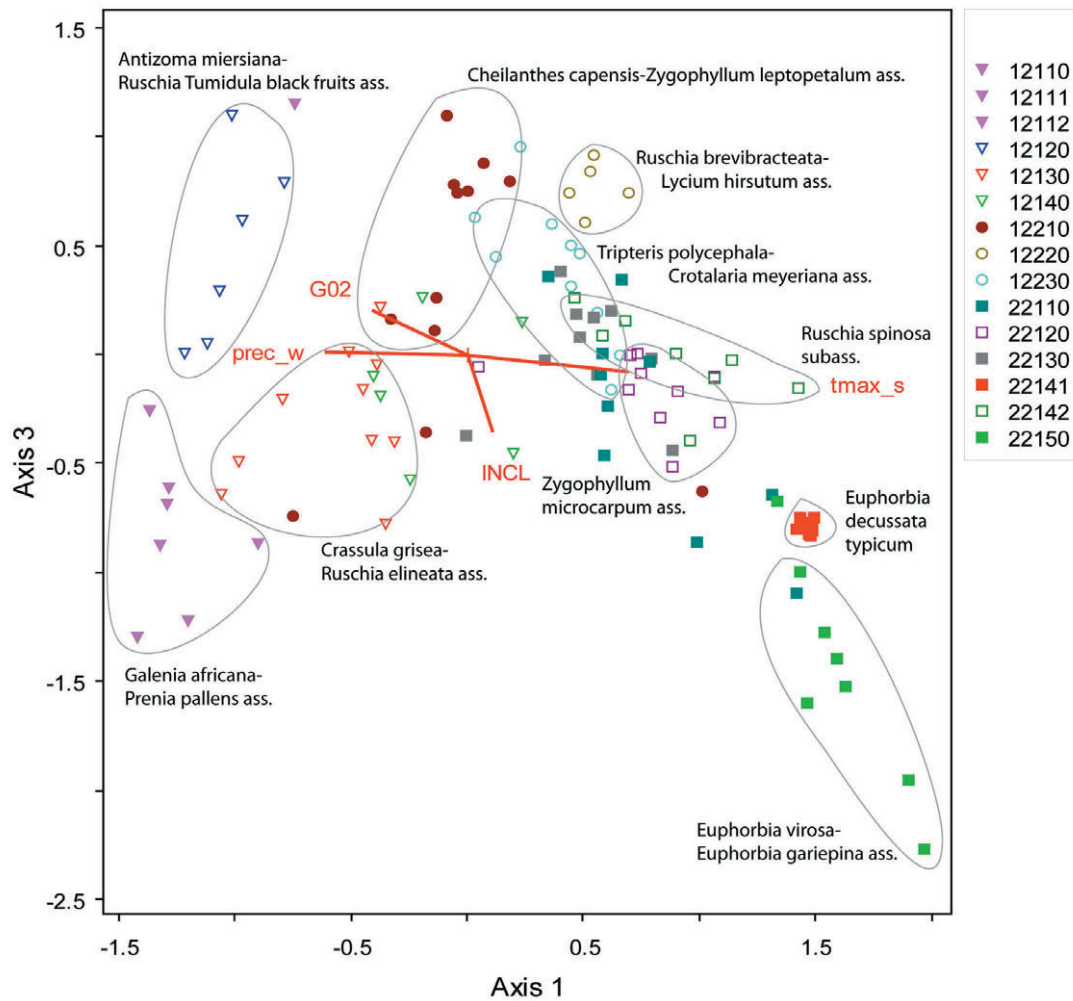


Fig. 3.20: Biplot of the Canonical Correspondence Analysis (CCA) for the slope habitats of the Richtersveld mountain region, axis 1 and 3. Numerical code and environmental variables as in Fig. 3.19.

### 3.2.6 Data set of the Succulent Karoo slope habitats

(A. 9, Fig. 3.21)

Within the CCA, with the Succulent Karoo slope habitats only, the communities of the escarpment range are clearly separated from the habitats of the Koeroegab mountains along the gradient of winter precipitation which follows axis one, explaining 25 %. Along the same axis the geological units separate the communities. The 'Crassula grisea - Ruschia elineata ass.', the 'Acrotome pallescens - Astridia alba ass.', the 'Cheilanthes capensis - Zygophyllum leptopetalum ass.' and the 'Ruschia brevibracteata - Lycium hirsutum ass.' on gray gneissic granite of the Vioolsdrif Suite (G08) are separated from

the 'Tripteris polycephala - Crotalaria meyeriana ass.' on mafic lava of the Orange River Group (G06) and from the 'Didelta spinosa - Helichrysum hebelepis ass.' and the 'Antizoma miersiana - Ruschia Tumidula\_black fruits ass.' on quartzite and sandstone of the Stinkfontein formation (G11). Along the third axis (18 % explanation) the exposition segregates the communities of the northerly exposition from the southerly, which is clearly visible on the different Koeroegab mountains exposures.

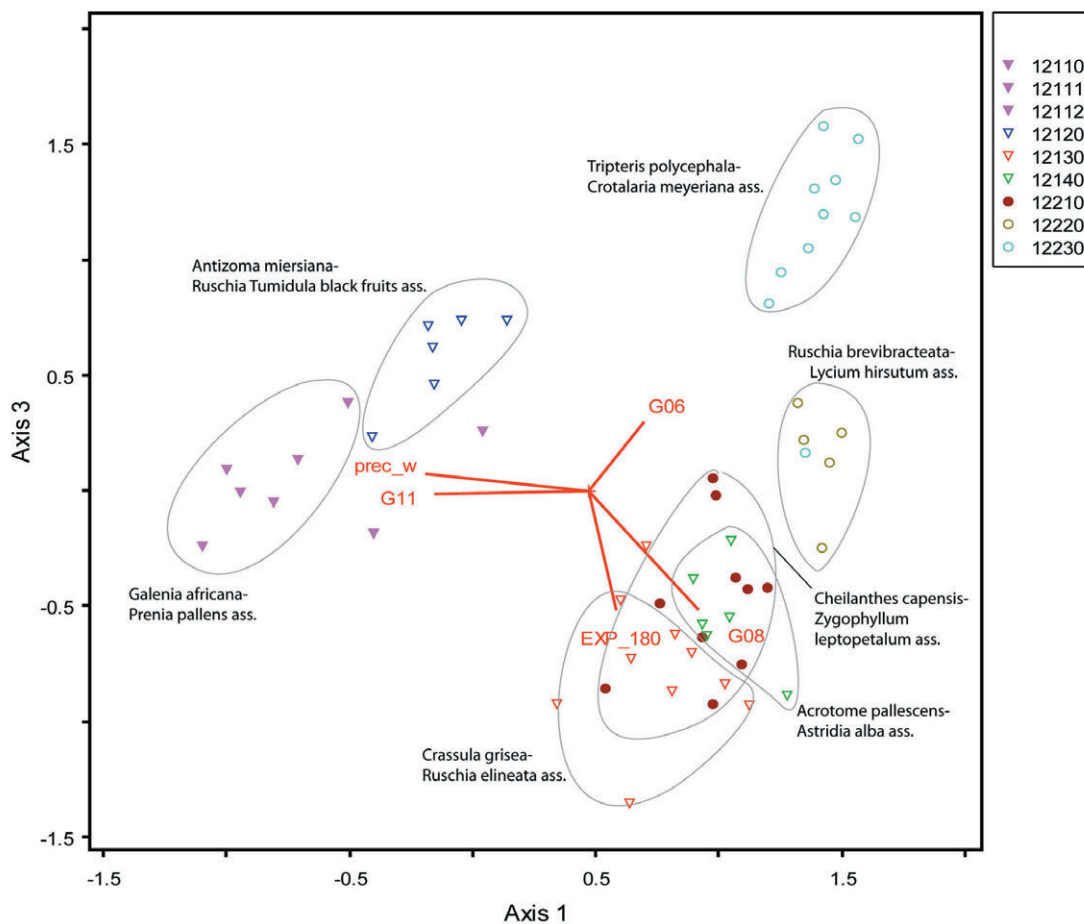


Fig. 3.21: Biplot of the CCA for the slope habitats of the Succulent Karoo. The number in the legend is the numerical code of the syntaxa: 1211 = *Galenia africana* - *Prenia pallens* ass.; 12111 = *Elytropappus rhinocerotis* - *Merxmuellera dura* sub-ass.; 12112 = *Pteronia divaricata* - *Berkheya canescens* sub-ass.; 1212 = *Antizoma miersiana* - *Ruschia Tumidula\_black fruits* ass.; 1213 = *Crassula grisea* - *Ruschia elineata* ass.; 1214 = *Acrotome pallescens* - *Astridia alba* ass.; 1221 = *Cheilanthes capensis* - *Zygophyllum leptopetalum* ass.; 1222 = *Ruschia brevibracteata* - *Lycium hirsutum* ass. and 1223 = *Tripteris polycephala* - *Crotalaria meyeriana* ass. The CCA is based on species cover and six environmental variables. Prec\_w = average monthly precipitation sum in winter; EXP\_180 = N/S exposition, G06 = mafic lava of the Orange River Group ; G08 = gray gneissic-granite of the Vioolsdrif Suite; G11 = on quartzite and sandstone of the Stinkfontein Formation.

### 3.2.7 Data set of the Nama Karoo slope habitats

(A. 10, Fig. 3.22)

The gradient of the maximum summer air temperature combined with the rainy days in winter, which decreases from the coast inwards, follows axis one (explaining 53 %) and clearly separates the more humid communities such as 'Brownanthus nucifer - Ruschia abbreviata ass.', the 'Zygophyllum microphyllum ass.' and the 'Pachypodium namaqua-

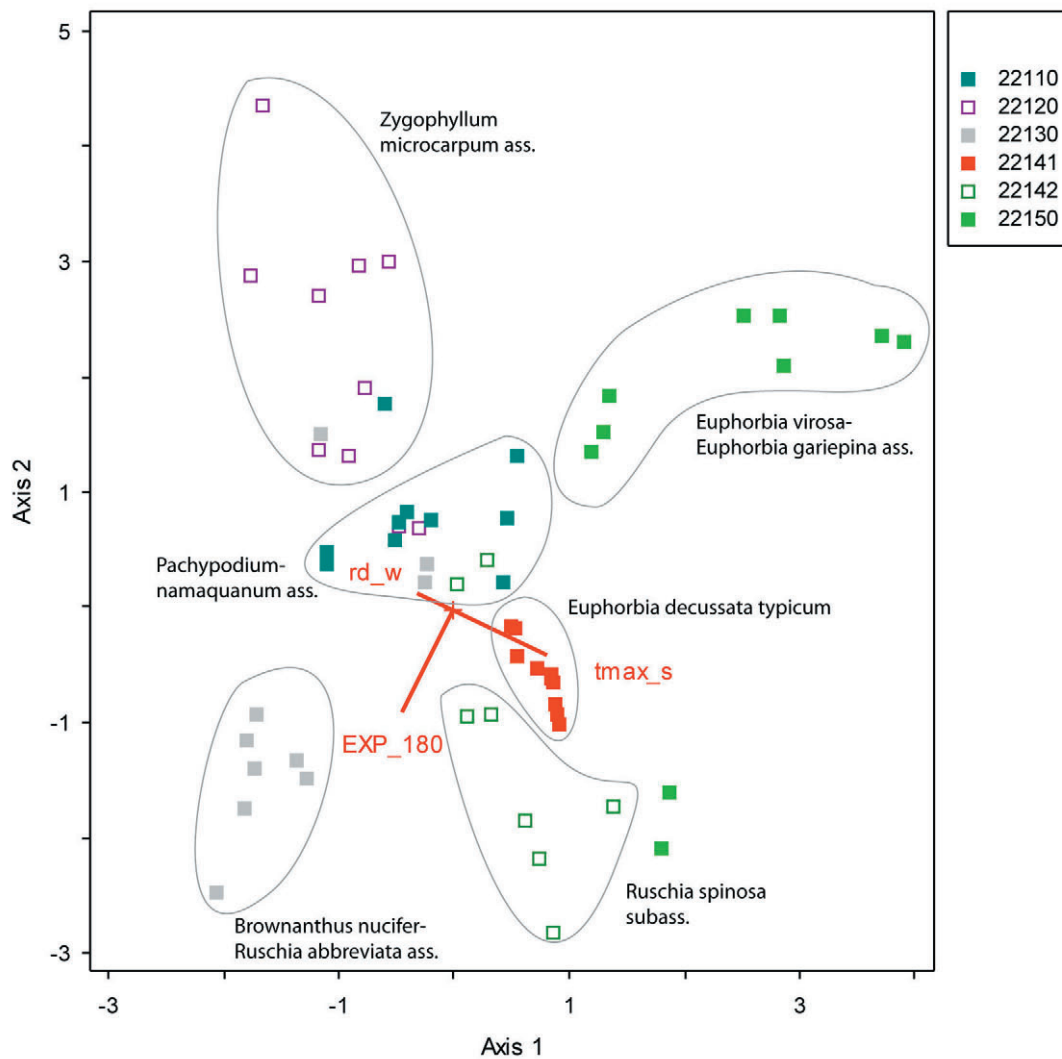


Fig. 3.22: Biplot of the Canonical Correspondence Analysis (CCA) for the slope habitats of the Nama Karoo. The number in the legend is the numerical code of the syntaxa: 2211 = *Pachypodium namaquanum* ass.; 2212 = *Zygophyllum microcarpum* ass.; 2213 = *Brownanthus nucifer* - *Ruschia abbreviata* ass.; 22141 = *Euphorbia decussata* typicum; 22142 = *Ruschia spinosa* sub-ass.; 2215 = *Euphorbia virosa* - *Euphorbia gariepina* ass. The CCA is based on species ground cover and four environmental variables. *Tmax\_s* = average monthly maximum air temperature in summer; *rd\_w* = average monthly rainy days in winter and *EXP\_180* = north-south exposition.

num ass.' from the arid communities in direct contact with the Oragne River valley such as 'Euphorbia virosa - Euphorbia gariepina ass.' and 'Euphorbia decussata ass.'. Along the second (25 %) and third axis (22 %) the exposition is the main variable, which clearly splits off groups of south exposed habitats with 'Brownanthus nucifer - Ruschia abbreviata ass.' and north exposed habitats with 'Euphorbia virosa - Euphorbia gariepina ass.'. The other communities lie in a central position. The first three axis, which together explain 100 %, excellently represent the main determining gradients such as maximum summer air temperature, exposition and rainy days in winter.

### 3.2.8 Data set of the flood plains and drainage lines

Only two variables remained after the tests for correlation and significance (A.11). The non-correlating variables, mean monthly maximum air temperature and sandy silt soil texture are significant with  $p \leq 0.005$ . Total winter precipitation, the geological units 'G06' und 'G04' and the silty fine sand were eliminated because of the low p-value.

The sum of all canonical eigenvalues of the CCA amount to 1.1. The eigenvalues of the first three axis are 0.63, 0.48 and 0.88. The first two axis explain 100 % of the species - environment relation, the first axis already explains 58 %.

The first axis correlates highly with the climatic variable, maximum air temperature (Fig. 3.23). Along this gradient the habitats of the Nama Karoo are separated from those of the Succulent Karoo. The 'Leucophrys mesocoma - Monechma mollissimum ass.' is situated on the left side of the axis that indicates lower maximum air temperature within the western part of the Richtersveld. 'Monechma spartioides - Cadaba aphylla ass.' is similar to the former Succulent Karoo community and is replaced by the Nama Karoo flood plain association 'Sisyndite spartea - Rogeria longiflora' further east, where the maximum air temperature is already higher. Further east, but on a higher altitude than the latter, the 'Prenia tetragona - Psilocaulon subnodosum ass.' occurs under the influence of the high maximum air temperature. The transition of the 'Monechma spartioides - Cadaba aphylla ass.' on flood plains and drainage lines within the Succulent Karoo to the 'Sisyndite spartea - Rogeria longiflora ass.' also follows an elevation gradient from about 500 m to 400 m and lower. The second axis is correlated with the soil texture sandy silt. It divides the footslope habitats from the habitats of the flood plains and drainage lines. The 'Euphorbia mauritanica\_Gariep - Zygophyllum decumbens ass.' shows more affinity to the Succulent Karoo, whereas the 'Adenolobus garipensis ass.' and the 'Calicorema squarrosa ass.' are characteristically Nama Karoo elements.

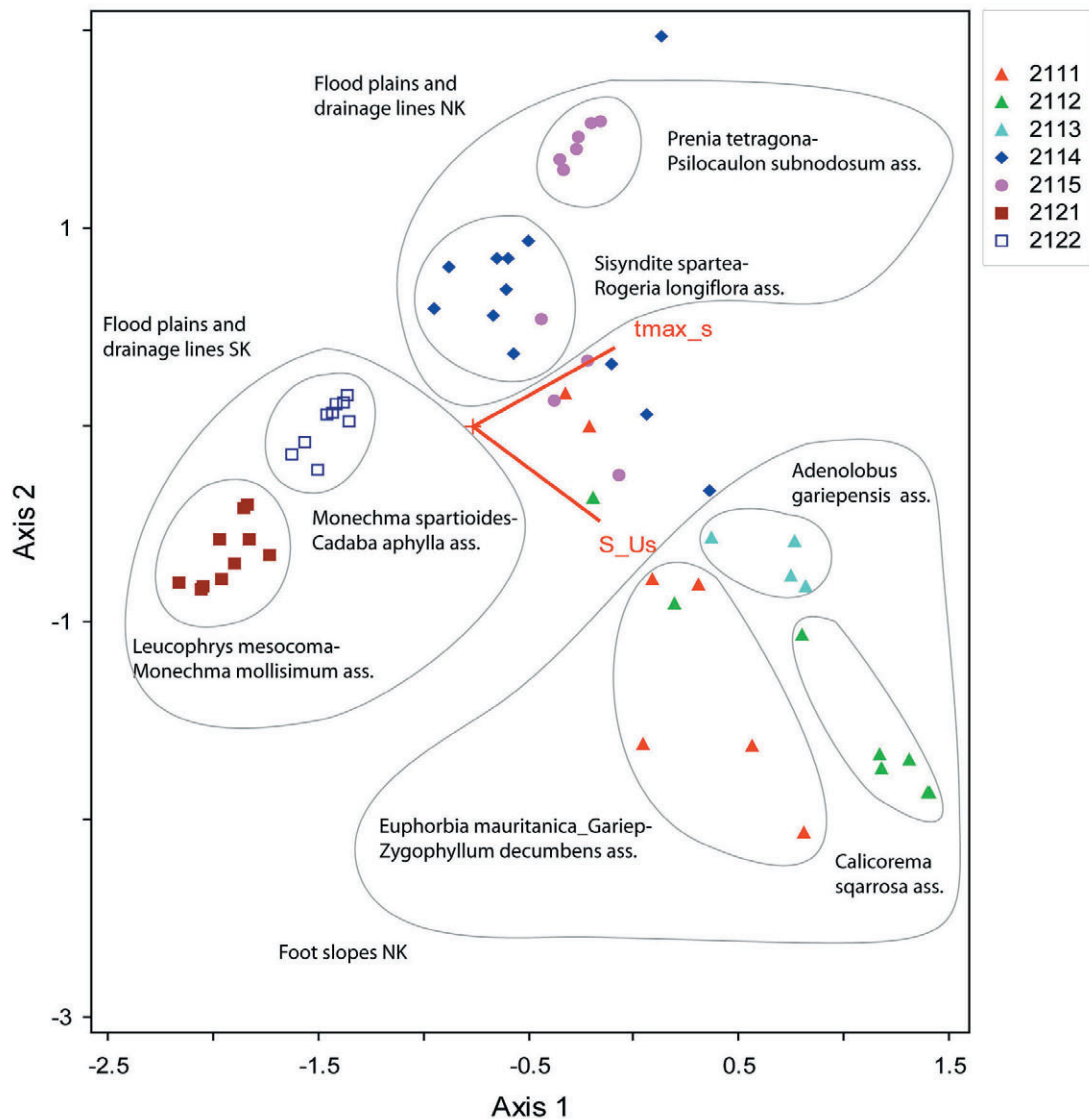


Fig. 3.23: Biplot of the CCA for the habitats of the flood plains and drainage lines. The number in the legend is the numerical code of the syntaxa: 2111 = *Euphorbia mauritanica\_Gariep - Zygophyllum decumbens* ass.; 2112 = *Calicorema squarrosa* ass.; 2113 = *Adenolobus gariepensis* ass.; 2114 = *Sisyndite spartea - Rogeria longiflora* ass.; 2115 = *Prenia tetragona - Psilocaulon subnodosum* ass.; 2121 = *Leucophrys mesocoma - Monechma mollissimum* ass. and 2122 = *Monechma spartioides - Cadaba aphylla* ass. The CCA is based on species cover and two environmental variables. *Tmax\_s* = average monthly maximum air temperature in summer; *S\_Us* = soil texture sandy silt.

### 3.2.9 Selected species - environment correlations

The differential species of the syntaxon 'order' already show a distribution focus along the climatic gradient (Fig 3.24). *Euphorbia ephedroides*, a typical species of the 'Tetragonia echinata - Pteronia glabrata ord.' (Habitats of the Succulent Karoo) has its distribution centre near the coast, where the precipitation is at a maximum within the



study area. The contrary is true for *Blepharis furcata*. This species is a differential species of the 'Sarcocaulon crassicaule - Blepharis furcata ord.' and has its distribution centre in the eastern part of the northern Richtersveld, where the precipitation maximum in winter is already low and the mean temperature in summer is high.

The high influence of the climatic factors is even more obvious on the 'alliance' scale (Fig. 3.25). The differential species of this syntaxon show a narrow distribution along the gradient from the coast further inland. The most dissimilar alliances with the highest distance to each other are the 'Eberlanzia ebracteata\_coast - Lebeckia multiflora all.' (Fig. 3.26). While it is mainly distributed on the escarpment on western exposures, where the highest precipitation values are reached, it shows a second distribution centre on the leeward side of the escarpment on southern exposures only on the highest peaks above 900 m.

Differences of exposition are expressed on the 'association' level. The southern and northern exposures show the most distinct differences. At Koeroegab, it could be observed that the 'Cheilanthes capensis - Zygophyllum leptopetalum ass.' is restricted to the south exposed slopes, represented by its differential species *Cheilanthes capensis* (Fig. 3.27). On north exposed slopes the 'Tripteris polycephala - Crotalaria meyeriana ass.' prevails.

The most extreme, with respect to aspect differences, could be seen for the Pooitjiespramberge in the western Gariiep (Fig. 3.28). Two alliances, of two different floristic regions, Succulent Karoo and Nama Karoo, occur on slope habitats facing each other. The 'Acrotome pallescens - Astridia albida ass.' of the Succulent Karoo appears on southern aspects whereas the 'Zygophyllum microcarpum ass.' of the Nama Karoo is restricted to northern exposures.

In the eastern Gariiep the 'Brownanthus nucifer - Ruschia abbreviata ass.' occurs on southern exposures (Fig. 3.29), whereas the 'Euphorbia virosa - Euphorbia gariiepina ass.' is mainly restricted to north exposed slopes.

Fig. 3.30 shows the course of the most important climatic factors along the coast-inland transect. The habitats near the coast, on the escarpment ('*Didelta spinosa* - *Helichrysum hebelepis* all. '), receive the most winter rain and the maximum summer temperature which reaches the lowest values within the study area. The habitats of the Nama Karoo slopes in the eastern Gariiep ('*Ceraria namaquensis* - *Aloe dichotoma* all. '), that are situated near the Orange River valley, recorded the highest maximum air temperature in summer and the lowest precipitation values in winter.

The stone content in the soils is negatively correlated with the winter precipitation. The highest stone content values were found in the soils of the eastern Gariiep (on slope habitats and on flood plains and drainage lines) where the lowest values of winter rain and the highest maximum air temperature in summer are to be found (Fig. 3.31).

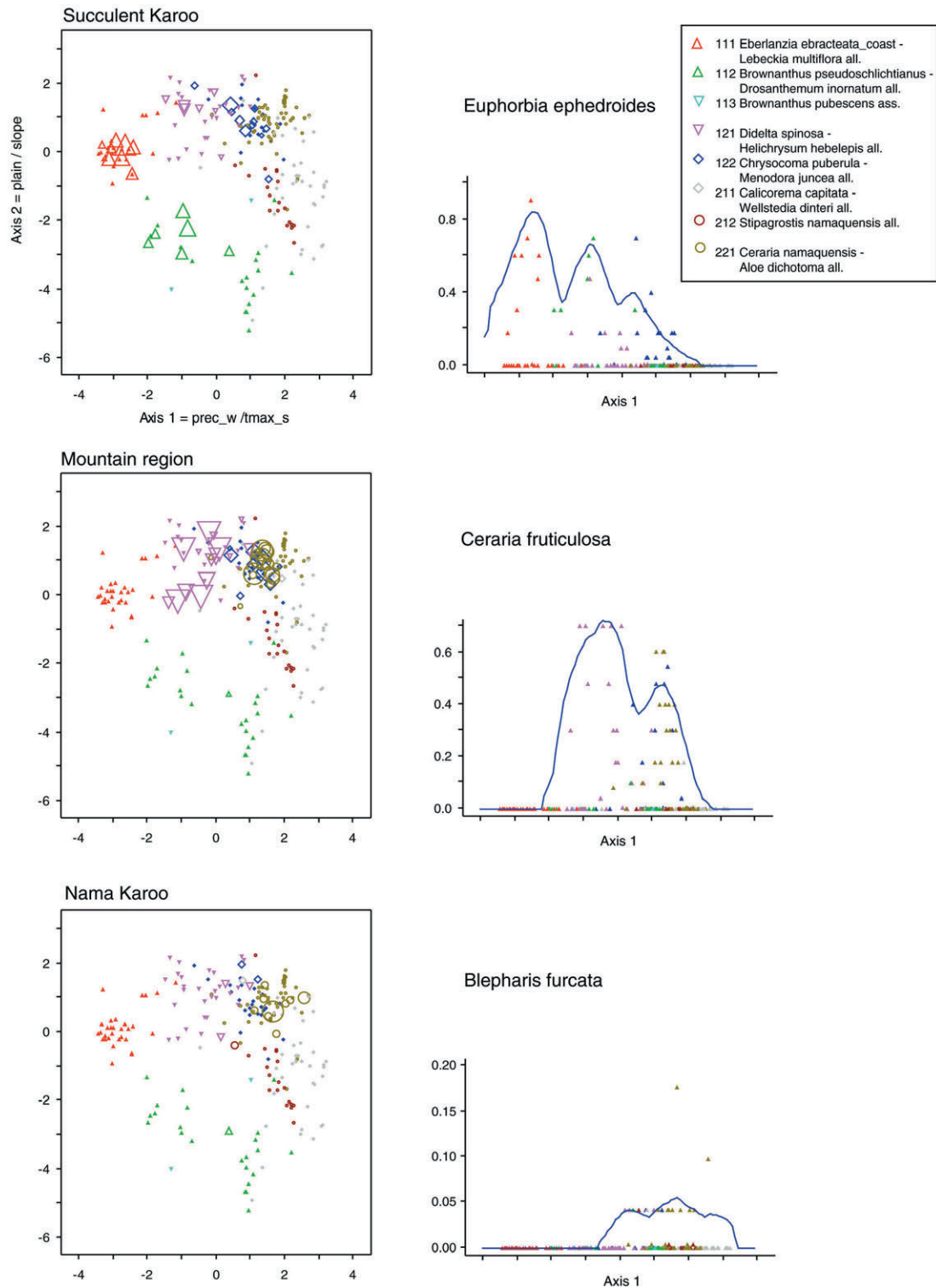


Fig. 3.24: Ordination (CCA) and side scatter plots of differential species with species abundance as a function of ordination axis scores; comparison within the order level.

The left graphs show the sample sites in ordination space of the CCA for the data set of all 230 classified relevés. The size of the symbols is proportional to the abundance of the regarded species within the plots.

The scatter plots to the right show the relationship between the abundance of the regarded species (y-axis) and the axes scores of the CCA ordination (x-axis). Axis 1 represents the variable precipitation in winter.

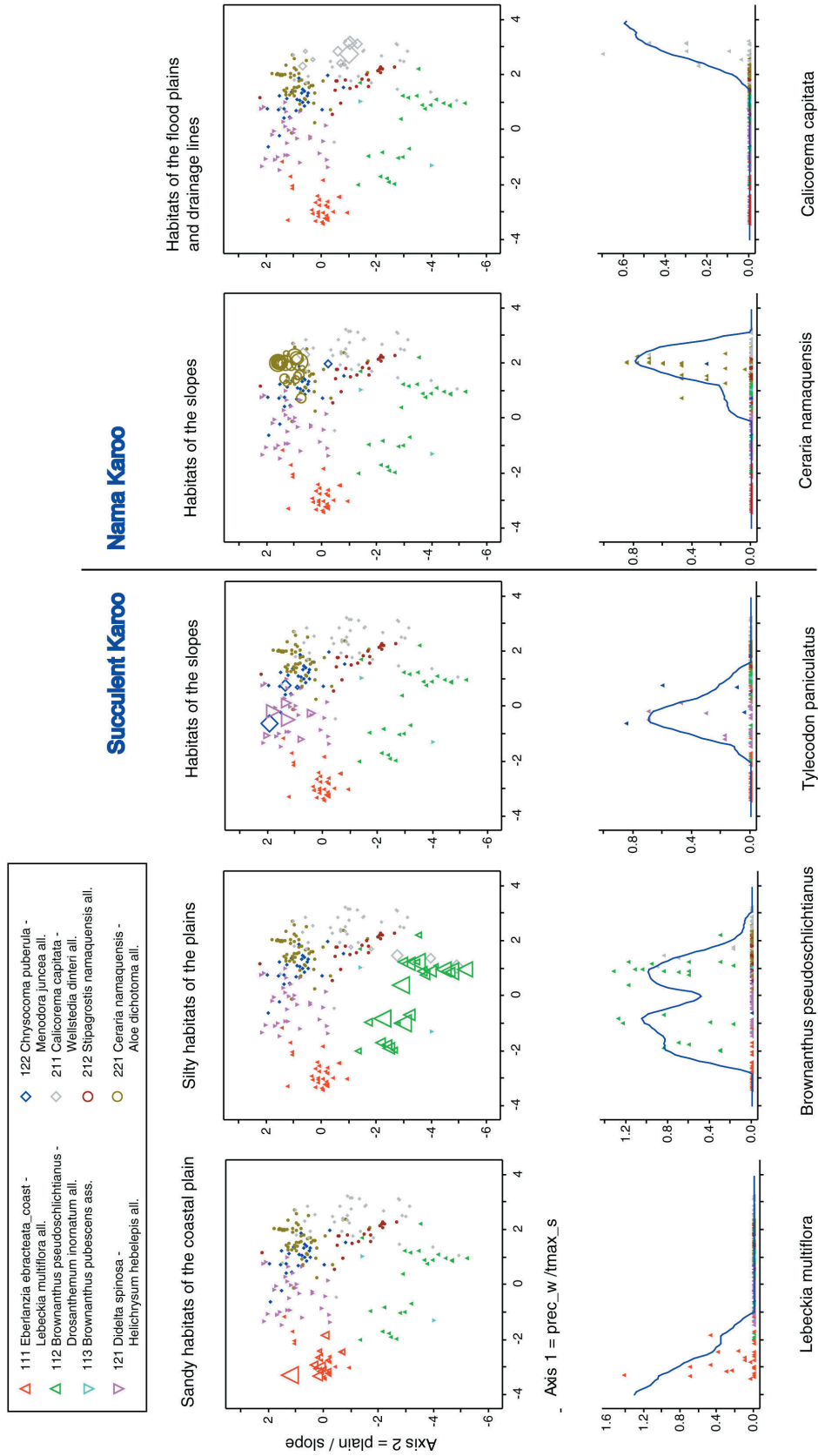


Fig. 3.25: Ordination (CCA) and side scatter plots of differential species with species abundance as a function of ordination axis scores; comparison within the alliance level. The upper graphs show the sample sites in ordination space of the CCA for the data set of all 230 classified relevés. The size of the symbols is proportional to the abundance of the regarded species within the plots. The scatter plots below show the relationship between the abundance of the regarded species (y-axis) and the axes scores of the CCA ordination (x-axis). Axis 1 represents the variable precipitation in winter.

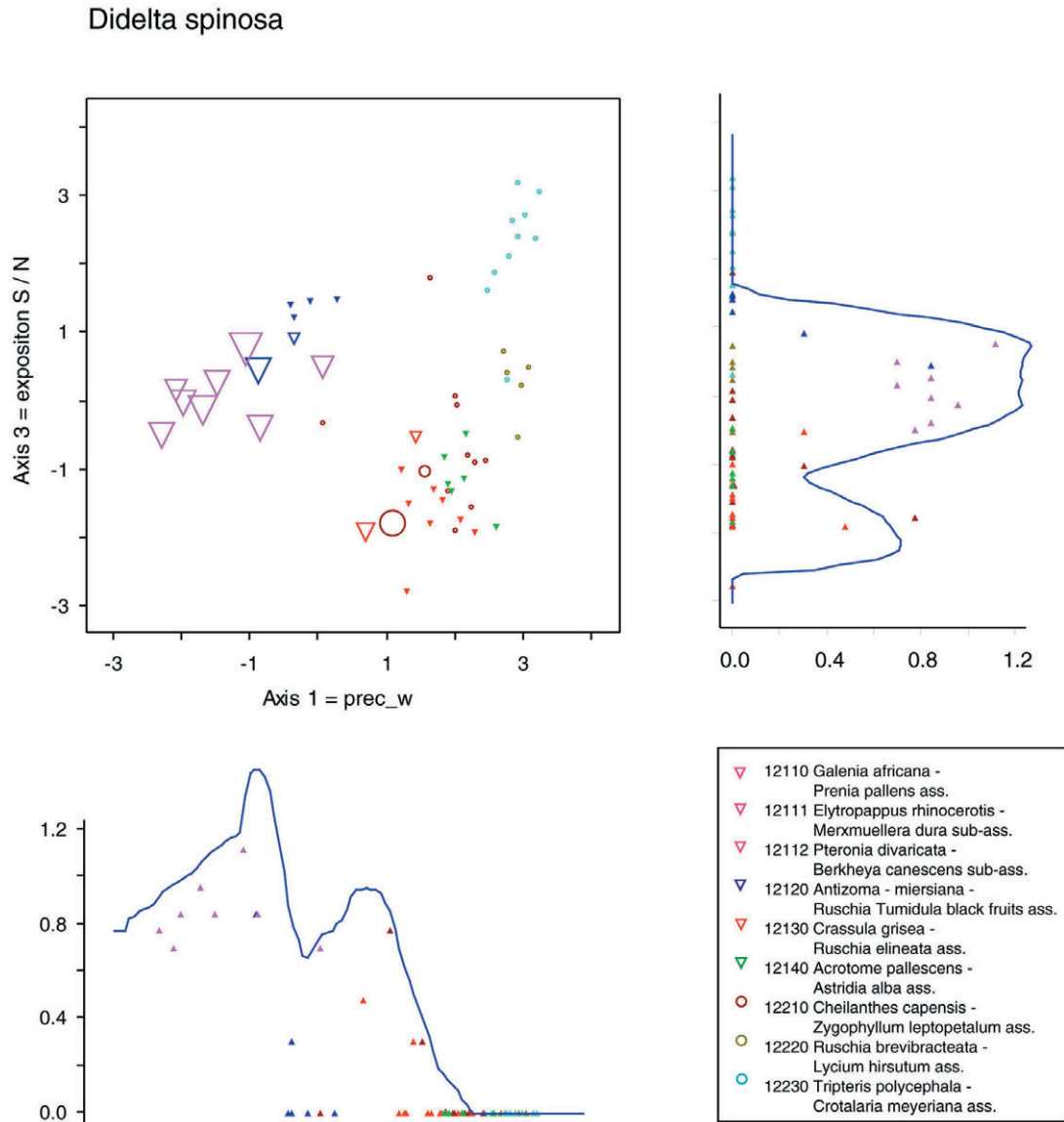


Fig. 3.26: Ordination (CCA) and side scatter plots of *Didelta spinosa* with abundance as a function of ordination axis scores; comparison within the alliance level.

The upper left graph shows the sample sites in ordination space of the CCA for the data set of all 230 classified relevés. The size of the symbols is proportional to the abundance of the regarded species within the plots.

The scatter plots to the right and bottom show the relationship between the abundance of the regarded species (y-axis) and the axes scores of the CCA ordination (x-axis). Axis 1 represents the variable precipitation in winter, axis 3 represents the south-north exposition (S / N).

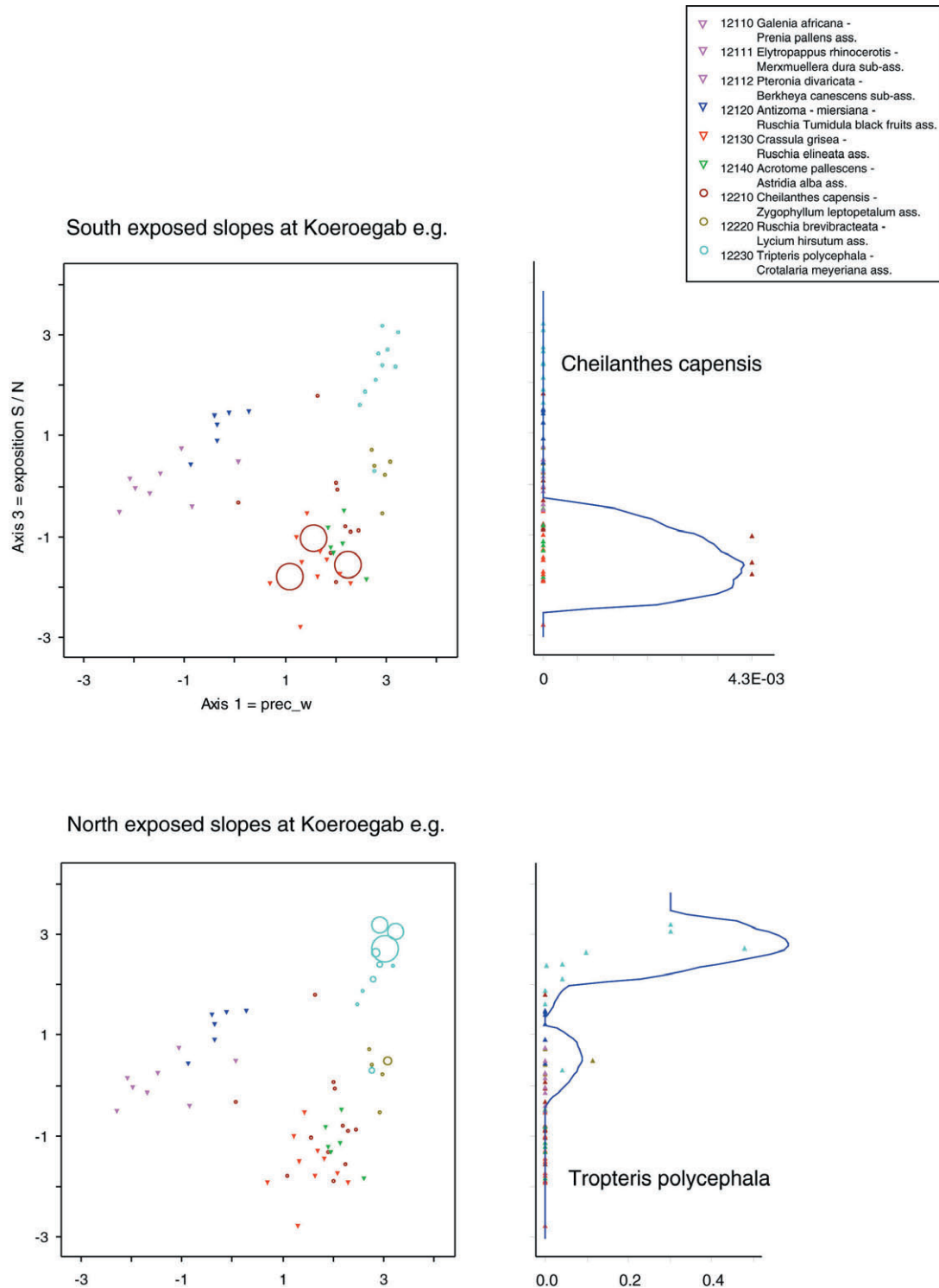


Fig. 3.27: Ordination (CCA) and side scatter plots of two differential species with abundance as a function of ordination axis scores; comparison within the association level: N/S exposure, e.g. at Koeroegab.

The left graphs show the sample sites in ordination space of the CCA for the slope habitats of the Succulent Karoo. The size of the symbols is proportional to the abundance of the regarded species within the plots.

The scatter plots to the right show the relationship between the abundance of the indicated species (y-axis) and the axes scores of the CCA ordination (x-axis). Axis 1 represents the variable precipitation in winter, axis 3 represents the south-north exposition (S / N).

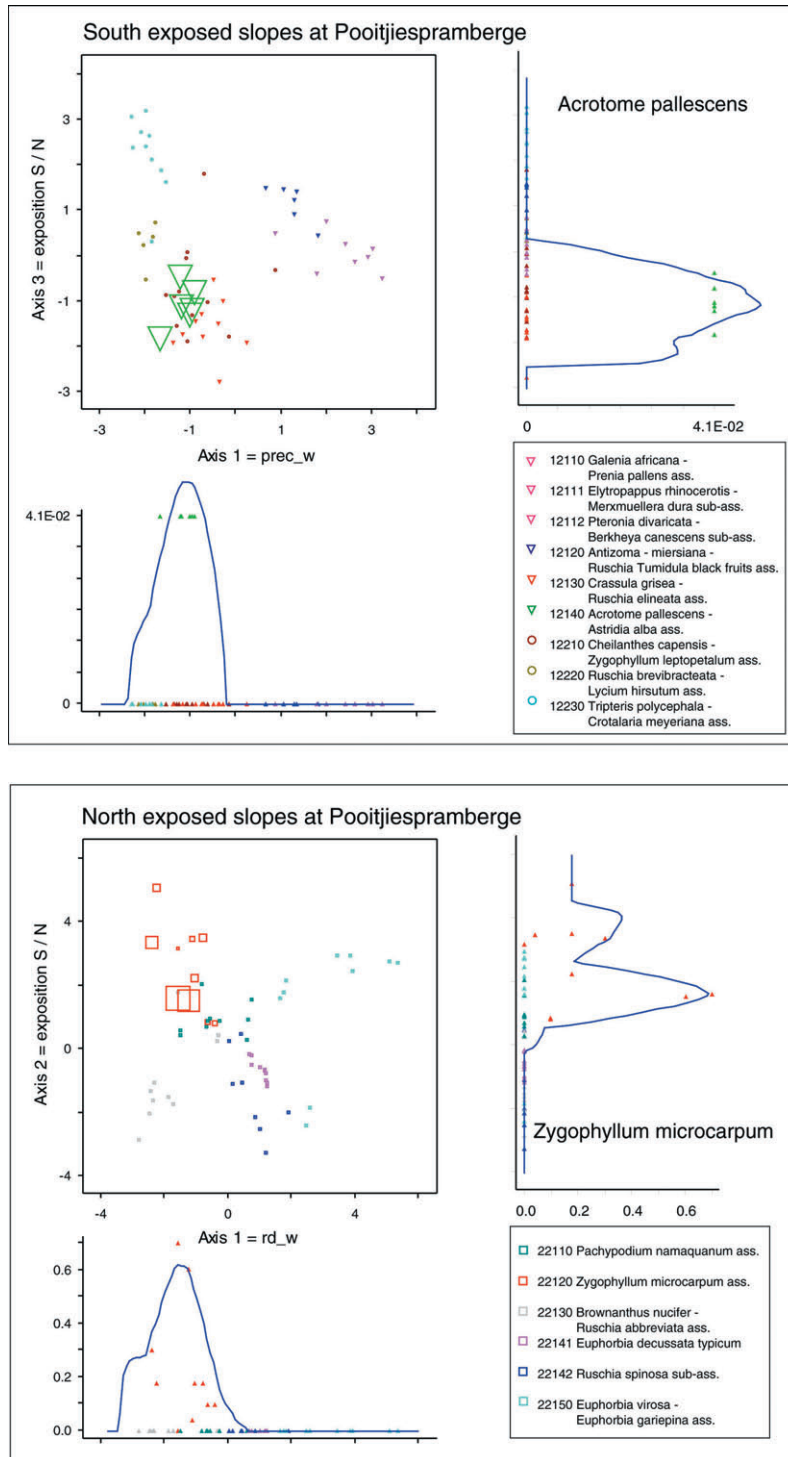


Fig. 3.28: Ordination (CCA) and side scatter plots of two differential species with abundance as a function of ordination axis scores; comparison within the association level: north-south exposure (exposure N/S), e.g. at Pooitjiespramberge.

The left graphs show the sample sites in ordination space of the CCA for the slope habitats of the Nama Karoo. The size of the symbols is proportional to the abundance of the regarded species within the plots.

The scatter plots to the right and below the ordinations show the relationship between the abundance of the indicated species (y-axis) and the axes scores of the CCA ordination (x-axis). Axis 1 represents at south exposure the variable precipitation in winter and at north exposure the variable rainy days in winter, axis 3 represents the south-north exposition (S / N).

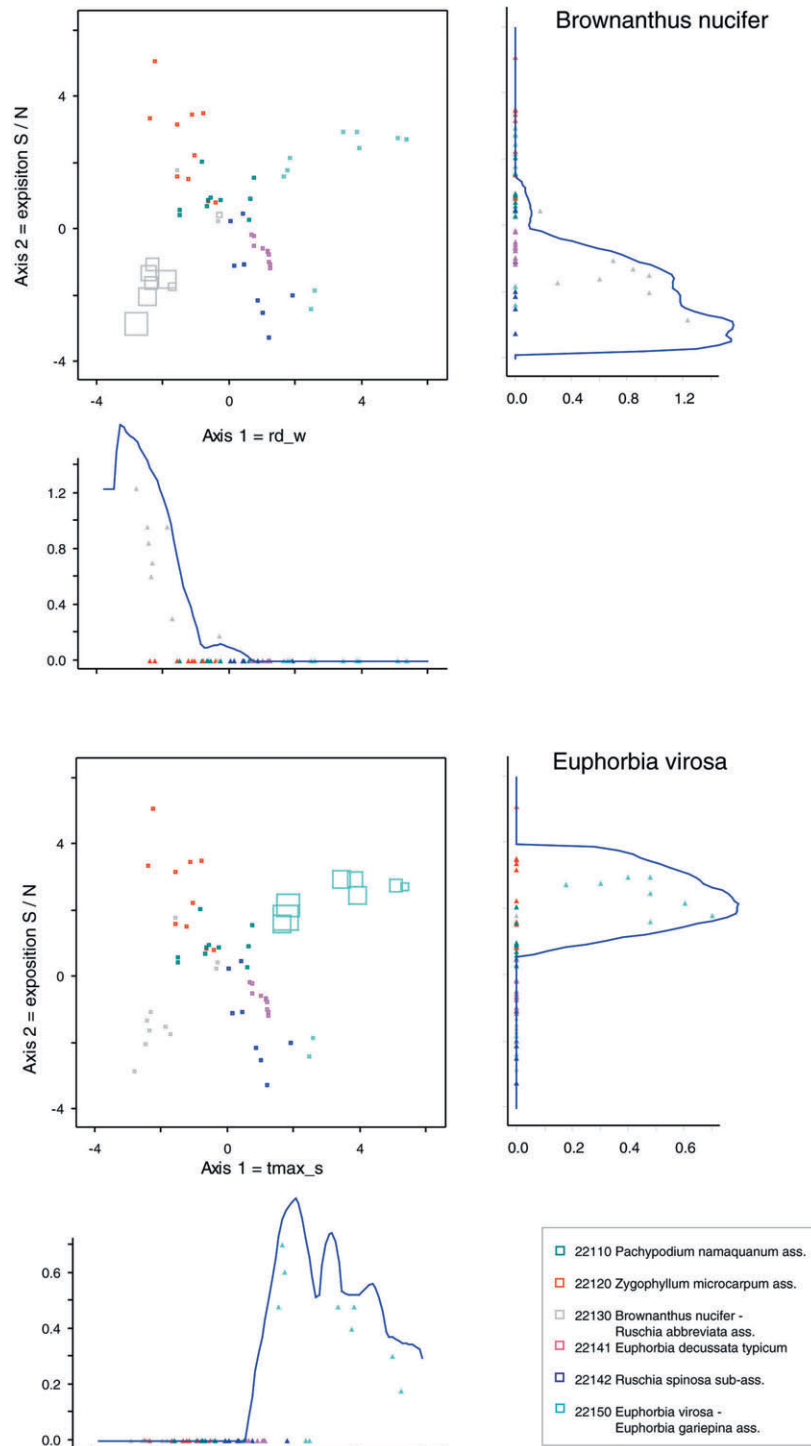


Fig. 3.29: Ordination (CCA) and side scatter plots of two differential species with abundance as a function of ordination axis scores; comparison within the association level: south facing slopes, *Brownanthus nucifer*, north facing slopes, *Euphorbia virosa*.

The central graphs show the sample sites in ordination space of the CCA for the slope habitats of the Nama Karoo. The size of the symbols is proportional to the abundance of the regarded species within the plots.

The scatter plots to the right and below the ordination show the relationship between the abundance of the indicated species (y-axis) and the axes scores of the CCA ordination (x-axis). Axis 1 represents at south exposure (*Brownanthus nucifer*) the variable rainy days in winter and at north-exposure (*Euphorbia virosa*) the variable precipitation in winter.

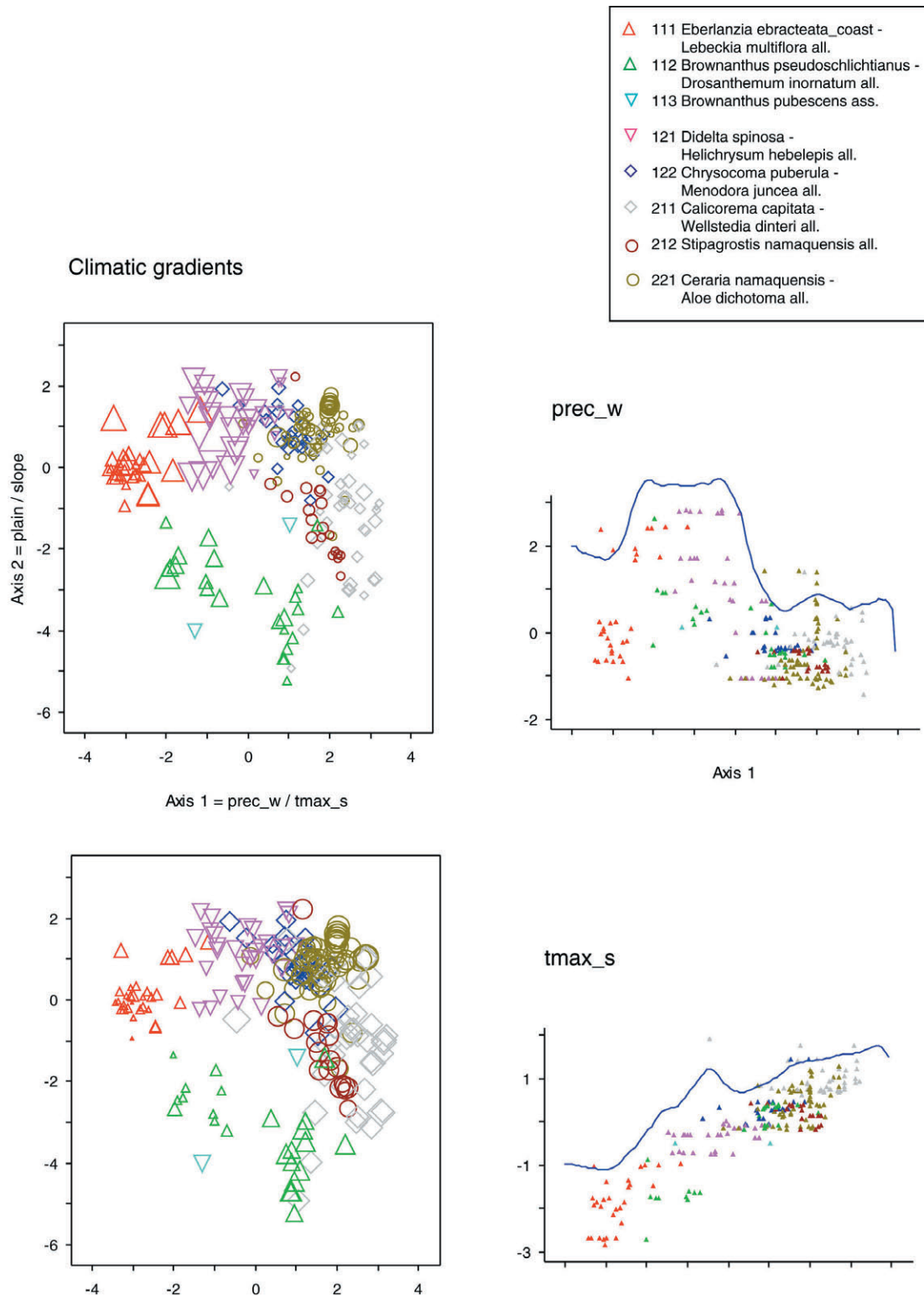


Fig. 3.30: Ordination (CCA) and side scatter plots of two climatic variables, precipitation in winter and maximum air temperature in summer. The left graphs show the sample sites in ordination space of the CCA for the data set of all 230 classified relevés. The size of the symbols is proportional to the amount of the regarded variable within the plots. The scatter plots to the right show the relationship between the value of the indicated variable (y-axis) and the axes scores of the CCA ordination (x-axis).



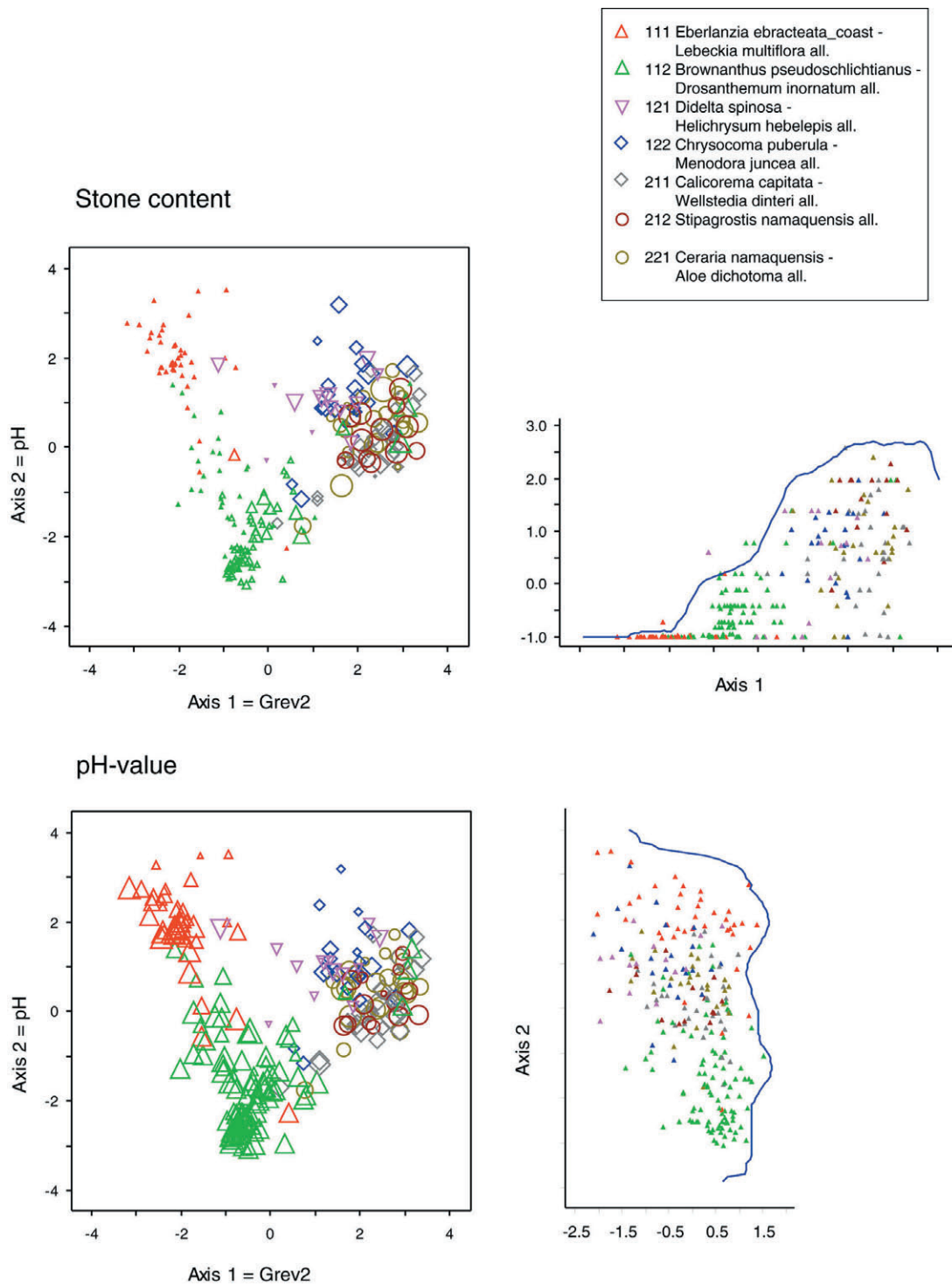


Fig. 3.31: Ordination (CCA) and side scatter plots of two soil variables, pH-value and stone content.

The left graphs show the sample sites in ordination space of the CCA for the slope habitats of the Nama Karoo. The size of the symbols is proportional to the amount of the regarded variable within the plots.

The scatter plots to the right show the relationship between the value of the indicated variable (y-axis) and the axes scores of the CCA ordination (x-axis).



## 4. Discussion

### 4.1. Environmental control of the spatial vegetation patterns

#### *Climate*

The effect of rainfall on species composition increases from more mesic areas to desert regions (Kadmon & Danin 1999). The limiting factor in dry areas is the water availability and other environmental factors are not as significant. Kadmon & Danin's proven hypothesis for the Israeli vegetation is also true for the semi-desert vegetation of the Richtersveld. The climate is the most important factor of the environmental inventory that controls the spatial patterns of the vegetation on a regional scale. It is represented by the total rain in winter and maximum air temperature in summer. Along both gradients the zonal vegetation is arranged from the coastline towards the interior (Fig. 3.11).

The dwarf shrub vegetation indicates the more humid habitats at the coast whereas the dry shrub vegetation indicates the dry habitats in the Orange River valley. Additionally the precipitation mainly determines the altitudinal zonation with the appearance of azonal vegetation elements on the escarpment (A. 3). The distribution of the vegetation represents the preliminary vegetation map of the northern Richtersveld (Fig. A. T8).

Transect studies along coast-inland gradients have been undertaken in both hemispheres offering a global comparison of ecological interrelation of environment and vegetation patterns. Vetass (1993) for example established for the vegetation distribution in north-eastern Sudan, that the humidity gradient correlates with the distance from the sea and distinguishes the communities as the primary gradient.

The Richtersveld transect is one of several coast-inland transects along which the vegetation and its determining factors were investigated from northern Namibia to southern South Africa. The west coast of southern Africa is of special interest because of the occurrence of two major climate regimes and their transition zone (Fig. 1.5). The winter rainfall zone is located at the Cape and extends to Namibia where it is restricted to a narrow strip directly at the coast. The summer rainfall zone is the main climate regime of South Africa that is adjacent to the winter rainfall zone via a small transition zone, the uniform rainfall zone (Werger 1986).

Becker & Jürgens (2000) investigated the vegetation along a west-east leading transect, approx. 150 km long, in the Kaokoland (Namibia) between S 17° and 19°30' latitude. This transect stretches parallel to the Richtersveld transect which is about 100 km long and lies further south between S 28° and 29° latitude. The authors also conclude a strong dependence of the vegetation occurrence and distribution on climatic factors. The generally east-west leading gradient of decreasing precipitation and increasing variability of rainfall determines the four main Savanna units of the Kaokoland. On the

basis of the absent winter rain, which does not reach that far north, the vegetation unit, which indicates the most humid habitats, is situated far inland, where the precipitation values of the summer rainfall reach up to 400 mm. The driest vegetation type covers the western part of the Kaokoland, where the precipitation reaches only 50 - 100 mm.

Further south, in the Central Namib Desert, the climate patterns and their impact on the vegetation were investigated by Hachfeld & Jürgens (2000) along a coast-inland transect between S 21° to 23° latitude. The Central Namib extends from the Atlantic Ocean in the west to the escarpment in the east at a distance of about 150 km from the coast. The coastal plain is characterised by mild air temperatures, continuously high air humidity as a result of fog and no rain. Contrary to this the continental eastern part of the desert shows high air temperatures, low air humidity and an increasing regularity of summer rainfall. The authors could prove a strong correlation between vegetation and climate with respect to species richness, total canopy cover, composition of growth forms and vegetation units. Winter rain occurs in a small belt near the coast as fog or fog drizzle. The monthly amount of precipitation measured 2 - 4 mm with a maximum of 25 mm in September 1998. This relatively high precipitation through fog allows the occurrence of leaf succulent chamaephytes directly on the coast. The high importance of fog can also be assumed for the coastal plain (Sandveld) of the Richtersveld.

The investigation along a 700 km long coast-inland transect at S 31°30' latitude (southward of the Richtersveld) found the mean annual saturation deficit of air moisture and rainfall reliability to be important predictors for various vegetation and plant characteristics (Werger & Morris 1991). The annual rainfall totals along the transect range from just over 100 mm to 325 mm. The gradient varies between low average annual rainfall directly on the coast to higher values on the escarpment. It drops again in the western part of the summer rainfall and increases gradually eastward. Therefore the transect leads from the winter via the uniform to the summer rainfall zone. The uniform rainfall zone forms a gap in the average annual rainfall. The duration of the frost period from zero on the coast to about 150 days at the eastern end of the transect rises steeply at the escarpment. Ratios of fresh weight to dry weight indicate the strong decrease in the succulence of the phytomass from the coastal zone to the summer rainfall zone.

Despite more arid conditions, the Richtersveld transect shows similarities to the transect further south. The winter rain still influences the vegetation patterns. Frost may also be a determining factor for the altitudinal vegetation zonation on the escarpment but with less significance. The transect leads, as does the transect southward, from the winter rainfall zone at the coast (Photo A. P3) to the uniform rainfall zone around the Orange River valley (A. P13). The adjacent summer rainfall zone was not part of this study (A. P19). The low precipitation amount in the uniform rainfall zone is intensified by the special situation of the steep carved Orange River valley, which is at a low altitude and is also situated in the rain shadow of the escarpment. This circumstance leads to high air temperature values and extreme dry conditions.

### Soil

The second most important factor that influences the vegetation distribution on a regional scale is the soil (Fig. 3.14, 3.15). Similar results were established by Roberts & Wuest (1999) for the distribution of plant communities in New Brunswick, Canada. The authors emphasized the overriding importance of climate and the secondary importance of soil factors in the controlling vegetation pattern on a regional scale.

Jürgens & Burke (2000) clearly showed that even the rudimentary soils of semi-arid regions, which accumulate in crevices and soil pockets on desert hill slopes are of high importance to vegetation.

The pH-value, which is highly correlated to the carbonate content, is the most important factor for the soil properties in the Richtersveld. The highest carbonate content is attained in the colluviums of the inner-mountain basins and the footslope plains of the escarpment range. On the coastal plain the carbonate and silt content together with the soil depth separate two different plant associations. The 'Cheiridopsis robusta - Ruschia leucosperma ass.' of the 'Brownanthus pseudoschlichtianus - Drosanthemum inornatum all.' on firm silty fine sand with high carbonate content borders on the 'Zygophyllum morgsana - Hermannia trifurca ass.' on deep medium sand with low carbonate content.

The higher pH-value of the silty fine sand of the footslope and inner-mountain plains of the escarpment could also indicate higher nutrient levels. Studies of soil chemical properties in the Namib Desert show that the soils of lower landscape positions have significantly higher nutrient levels than those of the dune sites (Abrams et al. 1997). However, the chemical soil analysis does not indicate higher nutrient contents for the silty fine sand of the lower footslope and inner-mountain plains compared to the higher slope positions in the Richtersveld (A. 13). The lowest pH-values are recorded on the western slope habitats that are exposed to the winter rain, where the leaching of salts is higher than for all other habitat types.

The relationship between the stone content and the predominating precipitation regime is obvious. The stone content increases with decreasing precipitation values from the west to the east of the Richtersveld mountains. Whereas chemical processes are part of weathering during winter under the winter rain regime, they are almost absent under the increasing influence of the summer rain regime, where the physical weathering leads to more coarse weathering products per time than the chemical weathering under water influence.

Besides the main controlling climate factors precipitation and air temperature, the stone content and soil texture could be responsible for the different vegetation cover of the silty plains and the gravelly plains. The silty plains in the western part are covered by the 'Brownanthus pseudoschlichtianus - Aridaria noctiflora s. noctiflora' formation. Whereas the gravelly flood plains in the eastern part carry the 'Stipagrostis obtusa com.' (Springbokvlakte) with low cover density. Or they are covered by the 'Prenia tetragona

- *Psilocaulon subnodosum* ass.' such as in the Kokkerbomkloof, which is located on the same elevation as the silty plain of the Koeroegabvlakte. The appearance of '*Brownanthus pseudoschlichtianus* - *Aridaria noctiflora* s. *noctiflora*' stands in the drier eastern part of the Richtersveld on remaining silty fine sand pockets in the shelter of rock outcrops and along footslopes or banks of drainage lines may be evidence for this assumption.

### *Geology*

The influence of the geology on the vegetation composition and distribution acts indirectly via soil properties. Burke (2002) investigated the effect of geology and derived land forms on properties of soil pockets on arid Nama Karoo inselbergs. She could prove that the underlying geology determines the physical and chemical soil properties. On basalt the content of clay, silt and organic matter, as well as the nutrients nitrogen, potassium, magnesium, sodium and calcium reaches the highest values of all other soils investigated in different geological units. Soils on sandstone, shale and breccia on the other hand show low clay, phosphorus and magnesium contents. The lowest silt, nitrogen, potassium and sodium contents were recorded in soils derived from granite. Such a detailed investigation of the geological influence on soil properties is absent for the Richtersveld. Even though there are several indications for the influence of the geological units on the vegetation patterns nevertheless it appears with lower significance than other factors. The '*Antizoma miersiana*-*Ruschia Tumidula\_black fruits* ass.', for example, only occurs on the fine-grained granite that weathers to large rounded boulders. This factor could not be established, as this is the only recorded location for this geological unit under a winter rain regime. More records on this geological unit would be necessary. Low silt and nutrient contents such as in soils on granite inselbergs were also recorded for the Goariep and Tatasberg granite.

The influence of the geology on the vegetation via the physical soil properties is also obvious at the fine grained granite sites of the Tatasberg Complex and the Goariep Mountain where the canopy cover between the large rounded boulders reaches higher percentage values than on other geological units.

### *Relief*

The influence of the relief is shown on a local scale. Besides the dominating climatic factors it is mainly the exposition and secondly the inclination which separates the associations of the slope habitats in the Richtersveld (Fig. 3.19). The altitude is highly correlated with the precipitation amount and air temperature and therefore also indirectly responsible for the regional vegetation distribution.

The northern and southern slope aspects reveal differences in vegetation cover and species composition. These effects are caused by micro-climatic differences. Northern exposition means sun-exposed in the southern hemisphere. Insolation and temperature and therefore the evapotranspiration are higher on northern than on southern slope

aspects. Exceptional aspect differences are to be observed in the western Gariep, for example, where the northern exposures are scarcely covered by Nama Karoo elements, whereas the south exposed slopes are densely covered by species of the Succulent Karoo. Kutiel & Lavee (1999) examined the effect of south and north facing hill slopes on soil and vegetation properties along a climatic transect in Israel, which covers the Mediterranean, semi-arid, arid and extreme-arid climatic zones. The authors could prove that, within the semi-arid zone, the differences between the aspects were the highest for soil moisture. Here, on the northern hemisphere, the north facing aspects are the most humid. The content of organic matter was also significantly higher ( $p \leq 0.05$ ) in the soils of north facing slopes. These more favourable conditions on northern exposures are also revealed in a higher vegetation cover, which is only significant ( $p \leq 0.05$ ) for the semi-arid and Mediterranean sites. Kutiel and Lavee could also observe a floristic difference between south and north facing slopes in the semi-arid zone. The north facing slopes were dominated by Mediterranean species, whereas the common species on the south facing slopes had Saharo-Arabian, Irano-Turanian, and Mediterranean affiliations.

It could be observed during the fieldwork in the Richtersveld, that the soils under the higher canopy cover on south exposed slopes in the Koeroegabvlakte are moist longer after precipitation by rain or fog than on the north exposed slopes, where the cover is scarcer and the vegetation height lower.

To sum up, one can say that the climatic factors precipitation in winter and maximum air temperature in summer are the main controllers of the spatial vegetation pattern on a regional scale within the northern Richtersveld. The climate, as the main controlling factor for vegetation patterns was established for the whole western coast of southern Africa and was even found in other arid regions.

The second factor that influences the vegetation on a regional scale is the soil. Acidity, stone content and soil texture are the main soil properties that further divide the vegetation communities. The stone consistence of the different geological units influences the vegetation indirectly via soil properties. On a local scale the relief was shown to be the controlling factor. The north-south expositions show obvious differences in vegetation cover and species composition.

## **4.2. Classification of the northern Richtersveld vegetation - problems and comparison**

The synoptic analysis, emphasized by the results of the statistical analyses, revealed a subdivision of the northern Richtersveld vegetation into five main groups on the basis of the prevailing habitat types, coastal plain, escarpment mountain range, inner-mountain basins, Gariep mountains and flood plains and drainage lines (A. T7).

The habitats on plains and basins of the Succulent Karoo (11) are represented by two alliances, 'Eberlanzia ebracteata coast - Lebeckia multiflora all.' on the coastal plain (111) and 'Brownanthus pseudoschlichtianus - Drosanthemum inornatum all.' within the inner-mountain basins and footslope plains of the escarpment (112). These alliances occur in the Namaqualand Sandveld District and the Richtersveld Mountain District of the Succulent Karoo within Jürgens (1991) floristic subdivision.

The slope habitats of the Succulent Karoo within the mountain area (12) are also subdivided into two alliances: 'Didelta spinosa - Helichrysum hebelepis all.' on the seaward habitats (121) and the 'Chrysocoma puberula - Menodora juncea all.' on the leeward habitats of the escarpment range (122). The alliance of these habitats corresponds to the Richtersveld Mountain District.

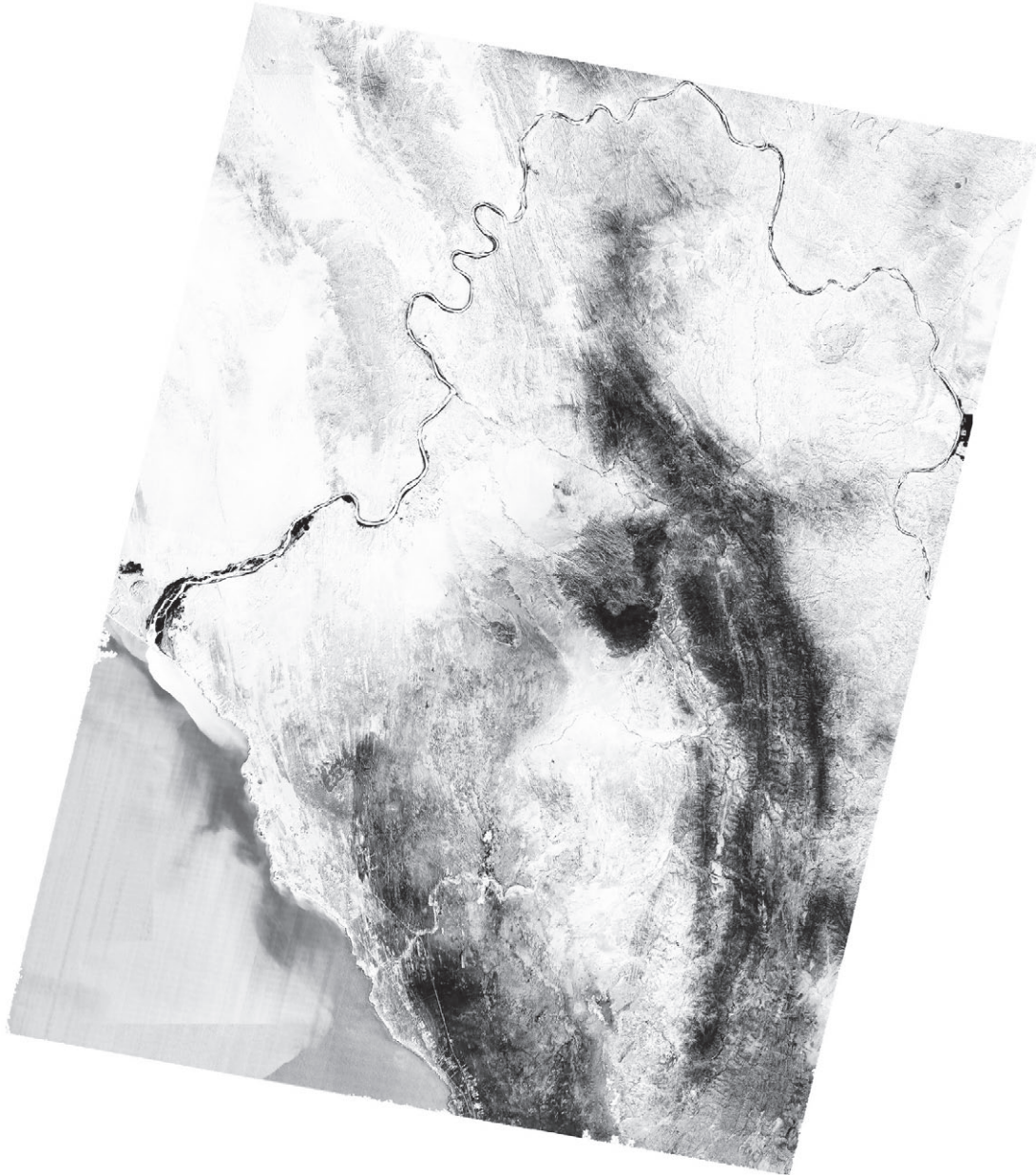
The slope habitats of the Nama Karoo within the mountain area (22) are only represented by one alliance, the 'Ceraria namaquensis - Aloe dichotoma all.' (221). The species of this alliance are part of Jürgens Eastern Gariep District of the Nama Karoo.

The habitats on gravelly flood plain and drainage lines (21) are subdivided into two alliances according to which floristic group they show affinities to. The 'Calicorema capitata - Wellstedia dinteri all.' is the typical formation on the gravelly flood plains and drainage lines in the eastern part of the Richtersveld with prevailing species of the Nama Karoo (211). Even the vegetation of the footslopes was ordered to this alliance in accordance to the floristic relationship. The 'Stipagrostis namaquensis all.' is accompanied by many species of the Succulent Karoo (212). Twenty-two associations were derived out of these six alliances.

The distribution of the vascular plant species does not occur in discreet communities. The vegetation change was continuous along the coast-inland gradients and along the altitudinal gradients. The subdivision of the vegetation into a hierarchical system was attempted in order to make the insight into the ecological correlations easier.

The species richness and canopy cover decreases from the coastal plain (mean number of species: 17, mean ground cover: 22 %) to the eastern Gariep (7; 8 %) with a peak on the escarpment mountain ranges (18; 26 (53 max.) %). Figure 4.1 shows the regions, where the vegetation density reaches the highest values discernible by the darker colour. Along the elongation of the Richtersveld transect species number and canopy cover increases further east to the Karasberg mountains (pers. obs.), where the dry shrub and dwarf shrub vegetation changes into an open Savanna type (Werger 1986, see photo A. P19). The dry shrub and dwarf shrub vegetation along the Orange River valley (eastern Gariep) dominated by *Euphorbia virosa* and *Euphorbia gariepina* with low species number and canopy cover (mean number of species: 3, mean ground cover: 3 %, Fig. 3.4) is part of the minimum zone according to Hachfeld & Jürgens (2000). They proved, for the northern Central Namib, that species number as well as total canopy cover of the plains show a distinct pattern with respect to coastal distance.





*Fig. 4.1: Enhanced satellite image of the northern Richtersveld showing areas of higher plant biomass density (black to dark grey colours). Parts of the coastal plain and the escarpment ranges show the highest canopy cover.*

Species number and canopy cover increases from the coast to 130 km further inland (7 to 33 species/0.1 ha and 11 to 35 %) with a depression between 35 and 75 km where the canopy cover reaches its minimum with values predominantly below 1 %. This part of the transect lies in the transition zone of the winter rain regime with fog precipitation and summer rain regime with convective rain. The high/Garua fog decreases to about 65 mm per year and the summer rain is almost lacking. The low precipitation value is coupled with high air temperature and low air humidity at this distance to the coast. The climate diagrams of winter and summer rain amount for the Richtersveld (Fig. A. 2) show

a gap in the area of 17°25' latitude where the Orange River flows south-northwards. Measurements for the fog precipitation are absent but it was observed that fog reaches the western part of the Gariep via the Orange River valley but seldom or never the eastern part. Hence, the macro-climatic situation of the Richtersveld is comparable to that of the northern Central Namib. The minimum zone is however situated further inland at a distance of 80 km from the coast owing to the greater extent of the winter rainfall zone, and the sudden rise of the escarpment functioning as a barrier to the rain.

*Problems of the classification in species poor and syntaxonomic incomplete treated areas*

The classification of species poor desert vegetation raises problems due to the fact that there are very few character and differential species available (Bornkamm & Kehl 1990, Burke 2002).

The given rules of the Braun-Blanquet system found satisfactory application in the western part of the Richtersveld, the Succulent Karoo, where species number and ground cover are sufficiently high. However, as previously mentioned, both values decrease from the western coast to the Orange River valley to the east (Nama Karoo). Hence, in some cases defined associations have only one character species and only one or no differential species or companions. These difficulties are well known from the northern hemisphere where Saharan vegetation was classified by Bornkamm and Kehl (1990) for example, who defined associations for the vegetation of the Western Desert of Egypt, or by Quézel (1965), who classified associations for the Saharan vegetation from Tchad to Mauritania and by Léonard (2001), who ordered the vegetation of the Jebel Uweinat (East Sahara).

The definition of character species forms another problem in syntaxonomically incomplete surveyed areas – appropriate for the western coast of southern Africa. The distribution of many species is poorly known and, even more so, their occurrence in the vegetation types. The diagnostic value of such species could change if it turns out that they are more widespread than expected. Thus diagnostic taxa given for any higher syntaxon might be subject to change.

As Dierschke (1994) mentioned, an inductive organized system such as the Braun-Blanquet system can only be slowly developed, progressively from more locally to inter-regional results. A further combination of larger areas has to lead to standardization and new evaluation.

From this point of view the proposal of a syntaxonomic classification for the vegetation of the northern Richtersveld given in this study is to be seen as a first approach. Phytosociological studies are locally restricted within the Succulent Karoo, Nama Karoo and southern Namib (see below). A general syntaxonomic classification is still absent. Therefore the classification system of Braun-Blanquet used, with its typical hierarchical structure, becomes more uncertain the higher the regarded level of hierarchy lies. Details

on class, order or alliance are preliminary in this study. For this reason a nomenclature, which follows the strict procedure of the 'Code of Phytosociological Nomenclature' (Weber et al. 2000), was not applied.

#### *Phytosociological comparison*

The first comprehensive and detailed description of the Richtersveld vegetation is given by Van Jaarsveld (1980), which was based on personal observations. Knapp (1968, 1973) gave a classification of the higher syntaxa of Ethiopia, Somalia, Natal, Transvaal, Kapland and some surrounding regions. The associations of the eastern and western Gariiep region in the Richtersveld are part of Knapp's succulent-rich dry forests (Euphorbio-Aloetia class), mainly of the *Aloetalia dichotomae* ord. at the lower Orange River of north-western South Africa and south-western Namibia. The extrazonal vegetation of the Orange River banks ('*Rhus pendulina* - *Ziziphus mucronata* ass.') belongs to the vegetation along drainage lines and dry rivers, *Tamarici* - *Salicetalia* (*Salicetea capensis* class), of the dry Karoo and the southern Namibia. The '*Monechma mollissimum* - *Leucophrys mesocoma* ass.' on drainage lines of the western Gariiep with *Schotia afra* is part of the dry shrub vegetation, *Schotio-Lycietalia* (*Schotio-Lycietea* class), of the Great and Little Karoo and surrounding areas. The '*Eberlanzia ebracteata*\_coast - *Lebeckia multiflora* all.' on sandy habitats of the coastal plain (Sandveld) belongs to the *Psilocalon*- and *Ruschia*-species rich succulent communities, (*Psilocalo-Ruschietea* class), mainly to the *Psilocalo* - *Ruschietalia* ord., at the coast of the Namaland within the western Kapland. The '*Tylecodon paniculatus* - *Osteospermum armatum* sub-ord.' on slope habitats of the Succulent Karoo are part of the open dwarf shrub communities, (*Pentzio-Pteronietea* class), mainly of the *Pentzio* - *Pteronietalia* ord., dominating in the central and western Karoo. The '*Zygophyllum morgsana* - *Hermannia trifurca* ass.' on the coastal plain (Sandveld) also belongs to the open dwarf shrub communities, to the *Chrysanthemoidetalia moniliferae* ord., dominating on sand dunes on the southern coast between the Cape Island and Port Elizabeth.

Werger (1986) represented greatly simplified formation classes in relation to the water factor that is of high importance for the vegetation structure. From the west coast to central southern Africa the succulent dwarf shrub vegetation is followed by the karroid dwarf shrub and open shrub vegetation with grasses. Further east the open Savannas appear with relatively tall grasses and widely spaced shrubs or low trees. Along major drainage lines dry gallery forest of low stature or open dry riverine scrub occurs. In the north with low or no precipitation the desert vegetation of the Namib can be found.

*Sensu* Werger (1986) the western part of the Richtersveld belongs to the succulent dwarf shrub vegetation and the eastern part to the karroid dwarf shrub and open shrub vegetation.

In the following, several locally restricted phytosociological studies that were developed within Wergers formation classes are represented and compared with the vegetation of

the Richtersveld (see Fig. 4.2 for a map with locations of the phytosociological studies in Namibia and South Africa). First the phytosociological studies that are located eastward of the Richtersveld, are described, then those, that lie south and northward.

1. The vegetation of Vaalputs in Bushmanland that was classified by Lloyd (1989a), shows floristic similarities to the Richtersveld vegetation. Vaalputs lies on the border between the rocky hills of Namaqualand and the flats of Bushmanland in the north-western Cape Province south-east of Springbok. The flat to gently undulating landscape on the Buschmanland Plateau lies between 1000 and 1030 m elevation. The vegetation shows high affinity to the Nama Karoo. *Sensu* Werger (1986) the vegetation belongs to the karroid dwarf shrub and open shrub vegetation. Lloyd distinguished four plant communities, which are highly correlated to soil properties (Lloyd 1989b):

- The *Aptosimum procumbens* v. *procumbens* dwarf /low semi-open// moderately closed shrub-land communities occur on calcrete and saline soils,
- the *Eberlanzia armata* low open//semi-open shrub-land communities appear on shallow soils overlying granite-gneiss basement or dorbank,
- the *Stipagrostis brevifolia* low/short open grassy shrub-land communities colonise soils mixed with aeolian sand and
- the *Stipagrostis ciliata* v. *capensis* low open grassland community cover the deeper, strongly acid aeolian sands.

Only 19 out of 284 (A. T7) species of the northern Richtersveld occur at Vaalputs, the genera counts 28 out of 143, but the coincidence on a family level is, with 14 out of 34, relatively high. The *Aptosimum procumbens* v. *procumbens* communities on calcrete soils show similarities to the plains of the Richtersveld with several leaf succulent chamaephytes of the genera *Brownanthus*, *Drosanthemum*, *Ruschia*, and *Psilocaulon*. *Salsola tuberculata* call to mind the sandy plains on the Sandveld where it is a frequent companion. It is a diagnostic species of the *Aptosimum procumbens* v. *procumbens* - *Salsola tuberculata* community at Vaalputs. The companions of this community such as *Chrysocoma ciliata* and *Zygophyllum retrofractum* are rare companions of the associations on the slope habitats in the Richtersveld mountain region. *Aridaria noctiflora*, one differential species of the 'Brownanthus pseudoschlichtianus - *Drosanthemum inornatum* all.' on silty sands of the inner-mountain basins in the Richtersveld, is also a diagnostic species of the *Aptosimum procumbens* v. *procumbens* - *Brownanthus ciliatus* s. *ciliatus* community in Vaalputs together with *Psilocaulon planisepalum*, *Galenia crystallina* and *Salsola zeyheri*. *Galenia crystallina* and *Prenia tetragona* appear with increasing sand and stone content as has been proved for the soils under the 'Prenia tetragona - *Psilocaulon subnodosum* ass.' in the east of the Richtersveld. *Salsola zeyheri* appears when the salt content in the soil increases as in Vaalputs.

The *Eberlanzia armata* communities on shallow sandy loam at Vaalputs call to mind the silty plain habitats of the inner-mountain basins near the footslopes in the

Richtersveld where *Eberlanzia ebracteata\_inland* appears with several species of the slope habitats on more sandy and shallow soils. The diagnostic species *Osteospermum sinuata* and *Eriocephalus ericoides* are common companions on the Nama Karoo slope habitats in the Richtersveld.

2. The karroid dwarf shrub and open shrub vegetation (Werger 1986) of the Augrabies Falls shows high similarities to the dry shrub vegetation of the eastern Gariep. The mountainous landscape is comparable to the Richtersveld with rocky outcrops or shallow soil on rock, sandy plains and alluvial deposits of the Orange River. Werger & Coetzee (1977) subdivided the vegetation into eight communities. The Augrabies

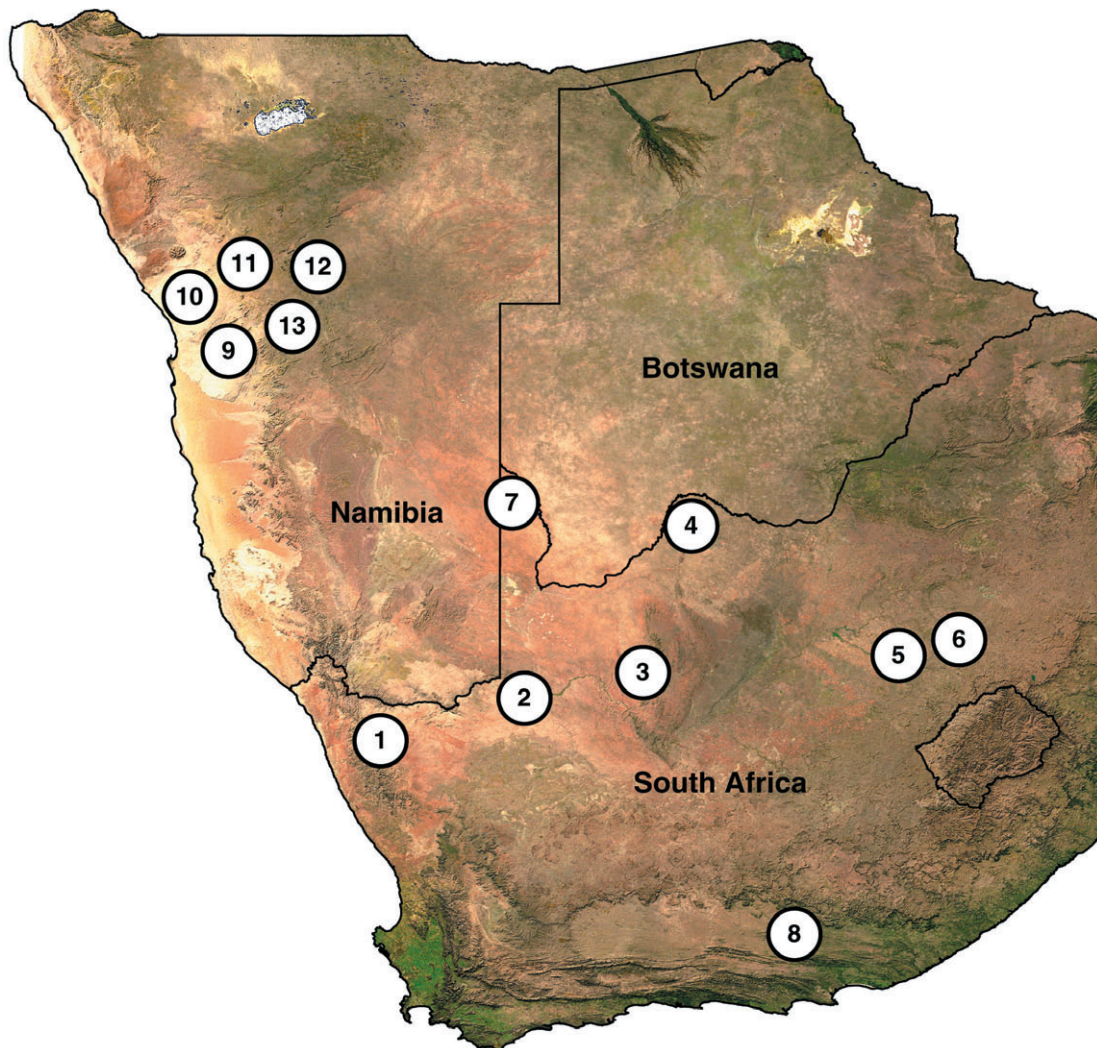


Fig. 4.2: Map showing locations of phytosociological investigations in southern Africa; numbers refer to the studies cited in the text.

Falls and Richtersveld vegetation share 39 species and 58 genera of 32 families. The *Ceraria namaquensis* community and the *Commiphora gracilifrons* community of the Augrabies Falls have some species, which also occur in the 'Ceraria namaquensis - *Aloe dichotoma* all.' of the Richtersveld eastern Gariep and the species-richer slopes of the Succulent Karoo. *Ceraria namaquensis*, *Commiphora gracilifrons*, *Hermannia stricta*, *Peliostomum leucorrhizum*, *Parkinsonia africana*, *Nimania capensis*, *Abutilon pycnodon* belong to the former. *Kleinia longiflora*, *Montinia caryophyllacea*, *Dyerophytum africanum*, *Rhus populifolius*, *Aptosimum spinescens*, *Indigofera pungens* and *Sarcostemma viminale* belong to the latter. The succulent dwarf shrub vegetation of the Succulent Karoo is absent in the Augrabies Falls vegetation. The species *Boscia albitrunca*, *Trichodesma africanum*, *Cleome angustifolia*, *Adenolobus garipina*, *Schotia afra*, *Sisyndite spartea*, *Monechma spartioides*, *Forsskaolea candida*, *Codon royenii* and *Rogeria longiflora* are species of the sandy and gravelly plains in both regions. In the northern Richtersveld they are joined in the 'Codon royenii - *Trichodesma africanum* sub-ord.'

3. The karroid dwarf shrub and open shrub vegetation (Werger 1986) of the Central Upper and False Arid Karoos (CUFAK) near the Orange River valley could be extrapolated over a wide adjacent area (Werger 1973b). The karroid communities were classified into the class *Pentzietea incanae* comprising five associations. Twenty-one species and 44 genera of 25 families are also recorded in the Richtersveld. The syntaxa of the Nama Karoo order 'Sarcocaulon crassicaule - *Blepharis furcata*' of the Richtersveld show similarities to those of the *Pentzietea incanae* class. However the habitats of the eastern Gariep (Nama Karoo) in the northern Richtersveld are not as species rich. Species of the *Zizipho - Rhigozeturum obovatii* association covering the dolerite slopes in the CUFAK, are only found along the Orange River banks in the drier northern Richtersveld. The *Monechmatetum incanii* association calls to mind the flood plains and drainage lines of the eastern and western Gariep.

4. Werger (1973) investigated the vegetation of the Tussen die Riviere Game Farm (TRGF) in the southern Orange Free State at the confluence of the Orange and Caledon Rivers. The TRGF is situated in the transition zone of the karroid dwarf shrub and open shrub vegetation of the grassland and (semi-aquatic) herbaceous vegetation (Werger 1986). Werger subdivided the vegetation into three major groups of communities; the riverine communities, the communities of the flats and gently sloping terrain and the communities of the steep slopes. The TRGF and the northern Richtersveld only share six species, but 44 genera of 21 families. The genera *Rhus*, *Diospyros*, *Lycium hirsutum* and *Acacia karoo* of the riverine communities occur, except the latter, on the slope habitats of the escarpment range in the northern Richtersveld. Half of the genera (25 out of 59) that occur within the communities of flats and gently sloping terrain are also common in the northern Richtersveld: *Osteospermum*, *Lessertia*, *Cyperus*, *Aptosimum*, *Salsola*, *Aristida*, *Dianthus*, *Euphorbia*, *Polygala*, *Helichrysum*, *Thesium*, *Gazania*, *Lotononis*, *Rhus*, *Sutera*, *Limeum* (*Limeum aethiopicum*), *Lycium*, *Chrysocoma*, *Pentzia*, *Indigofera*,

*Hermannia*, *Solanum*, *Geigeria*, *Eriocephalus* and *Asparagus*. The taxa of the communities of steep slopes *Gomphocarpus fruticosus*, *Selago albida*, *Rhus undulata* and *Hermannia cuneifolia* also occur on the slope habitats of the escarpment range in the northern Richtersveld.

5. The vegetation of the northern Orange Free State lies completely within the grassland vegetation of Werger (1986). Fuls et al. (1992) represented a classification of the vegetation on rocky outcrops with six associations of three alliances and one order. The study area is part of the Highveld inland plateau and forms a gently rolling land surface with elevations between 1300 m and 1700 m a.s.l. Two species and 34 genera of 19 families are still similar in both regions, Highveld and northern Richtersveld. The physiognomy of grassland is totally different to the vegetation formation of the Richtersveld, but on dry slopes and hills the occurrence of the species of the genera *Osteospermum*, *Blepharis*, *Felicia* and *Aristida* calls to mind the semi-desert slope vegetation.

6. Further east the grassland (*sensu* Werger 1986) of the north-eastern Orange Free State is floristically and physiognomically totally different to the west coast. Eckhardt et al. (1995) classified ten different grassland communities. Only one species (*Rhus discolor*) and seven genera of six families are similar to the northern Richtersveld.

7. The plant associations of the gently undulating sandy coastal plain (Sandveld) of the northern Richtersveld show some resemblance to the associations of the coarse sand of the dune tops and slightly undulating sand plains of the Kalahari. The vegetation is part of the open Acacia Savanna of the Southern Kalahari (Werger 1986). Leistner and Werger (1973) distinguished nine plant associations in the Southern Kalahari. Species of the *Monechma incanum* - *Stipagrostis ciliata* community and the *Peliostomum* - *Stipagrostietum obtusae* association also occur on the coastal plain on red sand in the 'Zygophyllum morgsana - *Hermannia trifurca* ass.': *Monechma incanum*, *Stipagrostis ciliata*, *S. obtusa*, *S. uniplumis*, *Limeum fenestratum*, *Grielum humifusum*, *Enneapogon desvauxii* and species of the genera *Hermannia*, *Indigofera*, *Aristida*, *Dimorphotheca* and *Tribulus*.

*Peliostomum leucorrhizum*, *Dicoma capensis* and *Trianthema triquetra* only occur in the eastern Gariep on slopes and plains.

8. The karroid dwarf shrub and open shrub vegetation *sensu* Werger (1986) is also part of the vegetation of the Karoo Nature Reserve (Cape Province). Palmer's (1989) phytosociological investigation reveals three different formations, the shrub-land, the succulent thicket and the dwarf shrub-land with eleven communities. The Karoo Nature Reserve surrounds the town of Graaff-Reinet at a distance of 200 km from Port Elizabeth on the Pacific coast. The altitude on the reserve varies between 850 to 1565 m. The northern Richtersveld and the Karoo Nature Reserve (KNR) share 12 species and 46 genera of 23 families. The shrub-land of the KNR occurs predominantly on uplands with sandstone and dolerite parent material. In the northern Richtersveld shrubs of the genera *Euclea*, *Maytenus* and *Acacia*, which are common in the KNR on high elevations, are

only found along drainage lines and on the Orange River banks. However, shrubs of the genera *Rhus* such as *Rhus undulata* and *Diospyros* also appear on the slope habitats in the Richtersveld, here on the escarpment range. The shrub-land of the rocky slopes and ridges at 1000 to 1300 m a.s.l. in the KNR shows floristic similarities to the slope habitats of the escarpment range at the same altitude in the Richtersveld. Dwarf shrubs of the genera *Hermannia* and *Euryops*, *Pentzia incana*, *Chrysocoma ciliata* and *Elytropappus rhinocerotis* and the succulent dwarf shrubs of the genera *Crassula*, *Lycium* and *Othonna cylindrica* are the taxa that belong jointly to both regions. However, succulence is a minor feature in the communities of the KNR in contrast to the communities of the Richtersveld slope habitats. The grassy shrub-land on dolerite at 1350 m a.s.l. is not represented on the high range of the Richtersveld escarpment. Only the genus *Merxmuellera*, which is also represented in the grassy shrub-land, occurs on the escarpment: *Merxmuellera dura* creates large patches on top habitats.

The succulent dwarf shrub-land of the KNR shows some similarities to those of the Richtersveld on the genus level. *Pachypodium*, *Blepharis*, *Eberlanzia*, *Mesembryanthemum* and *Psilocaulon* are represented in the Richtersveld as well.

9. The Tsaobis Leopard Park (TLP) of the Pro-Namib Desert Swakop River catchments, which is topographically comparable to the Richtersveld mountain region, also show floristic similarities to the vegetation of the northern Richtersveld. The basic formations of the TLP vegetation are the riparian woodland and the desert scrub (Cowlshaw & Davies 1997). The topographical range of the dominating mountains and ravines fringed by steep foothills and rolling plains varies between an altitude of 683 and 1445 m. The vegetation is part of Werger's (1986) karroid dwarf shrub and open shrub vegetation. Nine species and 20 genera of 16 families are similar to the northern Richtersveld. Mainly the nanophanerophytes such as *Boscia albitrunca*, *Euclea pseudebenus*, *Prosopis glandulosa* and *Tamarix usneoides*, found on drainage lines in the TLP, are also common on the drainage lines and flood plains of the northern Richtersveld. *Euphorbia virosa*, *Calicorema capitata* and *Monechma cleomoides* are mainly species of the eastern Gariiep slopes and footslopes, but the latter two species are common on the flood plains as well.

10. Burke (2002) recognized nine communities on the plains and inselbergs of the Central Namib. The study area lies in the southern Erongo region of Namibia. The altitude of the gently sloping landscape ranges from 700 to 1000 m. The granite domes and dolerite ridges of the inselbergs reach 20 to 470 m above the surroundings. The vegetation is part of Wergers (1986) desert vegetation of the Namib. Burke subdivided the vegetation of the plains and inselbergs into two main formations, grassland and shrub-land. On the inselbergs of the Central Namib many species occur that are characteristic for the escarpment zone or the highland Savanna (Giess 1971, 1981 in Burke 2002). Species of the genus *Commiphora*, *Euphorbia guerichana* and *Euclea undulata* are common and indicate better moisture supply, which allows the species to



extend their distribution into desert areas. The northern Richtersveld and the inselberg landscape of the Central Namib plains and inselbergs share eleven species, 16 genera of 13 families. Except *Euphorbia mauritanica* the species of the Central Namib which also occur in the Richtersveld are all part of the Nama Karoo associations. Species of the genera *Commiphora*, *Euphorbia virosa* and *Parkinsonia africana* are differential species and companions of the dry shrub vegetation in the eastern Gariep, Nama Karoo. *Ficus ilica*, *Maerua schinzii* and *Acacia erioloba*, which occur along drainage lines and ephemeral rivers in the Central Namib, also appear in the Richtersveld western Gariep, Nama Karoo along similar habitats.

11. The coast-inland transect at the northern Central Namib Desert, investigated by Hachfeld & Jürgens (2000) was already mentioned s.a. The study area is a weakly undulated and tilted plain. Only single inselbergs, granite outcrops and long-stretched dolerite ridges interrupt the vast plain, the sudden rise to the escarpment is absent. According to Werger (1986) the vegetation of the study area is part of the desert vegetation of the Namib. Species of the Succulent Karoo appear along a narrow coastal strip, whereas the plain further inland is inhabited by species of the Nama Karoo (Jürgens 1991). The classification compiled by Hachfeld (1996) and Hachfeld & Jürgens (2000) differentiates six major vegetation zones with 14 vegetation units. Taxa that occur in the northern Central Namib and in the northern Richtersveld amount to 17 species, 28 genera of 19 families. The species of the Central Namib plains such as the grasses *Aristida adscensionis*, *Enneapogon desvauxii*, *Stipagrostis ciliata*, *S. obtusa* and *S. subacaulis* and *Calicorema capitata*, *Cleome foliosa*, *Euphorbia phylloclada*, *Kissenia capensis*, *Monechma genistifolium*, *Zygophyllum stapffii* and *Tribulus zeyheri* are differential species or frequent companions on the plains of the western Gariep and eastern Gariep (Nama Karoo) in the Richtersveld. *Cleome semitetrandra* and *Monechma cleomoides* were observed on footslopes of the eastern Gariep, in which *Cleome semitetrandra* mainly occurs on gently sloped dolerite strips, which intrude into the older geological formation in several places. *Maerua schinzii* was recorded only once in the shade of the high granite boulders, outlier of the Goariep mountain, on the sandy coastal plain.

12. The vegetation of the flood plains and drainage lines in the eastern and western Gariep of the northern Richtersveld reveals floristic similarities with the vegetation of the washes, outcrops and sandy plains in the Central Namib. Robinson (1977) distinguished four major habitat types for the desert vegetation of the Namib (Werger 1986): salt marshes, pans, sand dunes and sandy plains-washes-rock outcrops-complex. Together 13 communities are defined. The Richtersveld flood plains and drainage lines share 31 species and 50 genera of 29 families with the sandy plains of the Central Namib Desert. The *Acacia erioloba* community of Robinson is comparable with the phanerophyte-rich banks of the lower Orange River, the 'Rhus pendulina- *Ziziphus mucronata* ass.' with *Acacia erioloba*, *Tamarix usneoides*, *Euclea pseudebenus*, *Ricinus communis* and *Nicotiana glauca*. The *Sesuvium - Stipagrostis obtusa* community with *Sesuvium*

*sesuvioides*, *Stipagrostis obtusa*, *Euphorbia phylloclada* and *Cleome diandra* is similar to the 'Stipagrostis obtusa com.' on the Springbokvlakte in the eastern part of the northern Richtersveld. The species *Monechma cleomoides*, *M. genistifolium*, *Tribulus zeyheri*, *Tripteris microcarpa*, *Forsskaolea candida*, *Trichodesma africanum*, *Dyerophytum africanum*, *Stipagrostis obtusa*, *S. ciliata*, *S. uniplumis*, *Enneapogon desvauxii* and *Tephrosia dregeana* joined in the *Monechma genistifolium* community, the *Petalidium variabile* community and the *Commiphora* - *Antheophora* community also occur in the northern Richtersveld. The majority are species of the flood plains and drainage lines ('*Codon royenii* - *Trichodesma africanum* sub-ord. '); some are also common on the slope habitats, mainly of the eastern Gariep.

13. The vegetation of the Naukluft Mountains shows high similarities to the Richtersveld mountain region. Burke (2001) defined 12 plant communities of Karoo shrub vegetation, which presents an isolated outpost of Nama Karoo vegetation. Within the formation system of Werger (1986) it belongs to the karroid dwarf shrub and open shrub vegetation. The Naukluft Mountains form the eastern outpost of the Namib-Naukluft Park. Burke recognized two different groups of communities, the communities of high altitude areas (> 1800 m) and the communities of lower altitude areas (< 1800 m). The amount of sharing species, genera and families of the Naukluft Mountains and the northern Richtersveld is 14, 24 and 15. *Pentzia spinescens*, *Eriocephalus ericoides*, *Lycium cinerum* and *Aptosimum spinescens* occurring on higher altitudes than 1800 m on the Naukluft Mountains are common species of the habitats on the escarpment range and the more favourite habitats of the eastern Gariep from about 500 to 1300 m. *Monechma cleomoides*, *Monechma spartioides*, *Zygophyllum microcarpum*, *Boscia albitrunca* and *Tribulus zeyheri* appearing under 1800 m on the Naukluft Mountains are mainly species of the drainage lines and flood plains up to 600 m. *Euphorbia virosa*, *Kleinia longiflora* and a *Commiphora* species occur mainly in the eastern Gariep, Nama Karoo. *Sarcostemma viminale* is common on low elevations of the escarpment range, Succulent Karoo.

In summary, one can say that a general phytosociological classification based on the Braun-Blanquet system is still lacking for southern Africa. However there are several phytosociological studies, which refer to restricted areas. Neighbouring areas of the Richtersveld are still absent e.g. the Ai-Ais Nature reserve and the Karasberg region of the Bushmanland or they are still under work i.e. the southern Namaqualand, which A. le Roux is dealing with. She investigated, for example, the Hester Malan Nature Reserve near Springbok (Roux 1984, PhD thesis). Under these circumstances the hierarchical classification of the Richtersveld vegetation can be seen as a preliminary approach. Higher syntaxa such as the level of 'alliance' or 'order' are uncertain because a comparison on a larger scale with neighbouring regions is not available at present. For this reason the syntaxon 'class' is not given. Werger (1973b) named a *Pentzietea incanae* class

comprising five associations for the karroid vegetation. The associations are described in a table but higher ranks such as alliance, order or class with their diagnostic species and characteristic species composition are not represented. A comparison on the syntaxa level order and alliance would give a more adequate result and probably an opportunity to re-rank the syntaxa found in the northern Richtersveld. The same problem is given to Knapp's classes and orders (1968, 1973). Only examples of characteristic species that belongs to these syntaxa are represented.

The syntaxa found in the northern Richtersveld show similarities to those represented below. However, there is no association or community, which is similar to those of the northern Richtersveld in its diagnostic species or its species composition. The similarities are briefly listed as follows:

The most similarities of the northern Richtersveld vegetation to the surrounding regions of southern Africa are found in Wergers (1986) karroid dwarf shrub and open shrub vegetation of the great Karoo area to the east and south.

The vegetation of the plains at Vaalputs are comparable to the silty plains of the coastal plain and inner-mountain basins belonging to the Jürgens (1991) Namaqualand Sandveld District and Richtersveld Mountain District of the Succulent Karoo Region.

The Augrabies Falls vegetation is highly similar to the slope associations in the eastern Gariiep, part of Jürgens Eastern Gariiep District of the Nama Karoo Region.

The vegetation at high elevations (1000 - 1300 m) of the Karoo Nature Reserve south-east to the Richtersveld reflect the association of the escarpment range at similar altitudes, which are part of Jürgens (1991) Richtersveld Mountain District.

Also similarities are obvious to Wergers (1986) desert vegetation of the sandy and gravelly plains of the Central Namib. Mainly the associations of the flood plains and drainage lines of the eastern Gariiep belonging to Jürgens (1991) Eastern Gariiep District of the Nama Karoo reflect the gravelly plains of the Central Namib.

The Sandveld (Namaqualand Sandveld District) of the Richtersveld show similarities to the Kalahari dunes.

Only low similarities can be seen for the grasslands and Savannas in the far east of southern Africa.

### **4.3. Life form spectra of the northern Richtersveld vegetation - in comparison with other deserts**

The life form spectra of the northern Richtersveld show the dominance of chamaephytes, followed by therophytes and phanerophytes. The presence of hemicryptophytes and geophytes is low. The amount of chamaephytes decreases from the coast to the eastern Gariiep, whereas the phanerophytes increase over the same section (Fig. 3.6). The therophytes reach the highest amount upon the plains (vlaktes). The mono-dominance of

chamaephytes is in accordance with the Sukkulent Karoo type of Rutherford's biome model (1997). The relatively high amount of therophytes shows the transition to the desert biome.

The growth forms leaf succulence and stem succulence show the same trend as the life forms chamaephytes and phanerophytes. Leaf succulence decreases from the coast to the eastern Gariep and stem succulence increases over the same section (Fig. 3.7).

*The life and growth form spectra mirror the influencing environmental factors*

The transition from winter to summer rain respectively from the Succulent Karoo to the Nama Karoo in the Richtersveld is reflected by the distribution of both, life forms chamaephytes versus phanerophytes and growth forms leaf succulence versus stem succulence. The growth form diversity of the northern Richtersveld is conspicuously high as is the species diversity. Cowling et al. (1994) established a significant positive relationship between species richness and growth form diversity.

Danin & Orshan (1990) investigated the distribution of Raunkiaer life forms along a climatic gradient in Israel. They could establish that the phanerophytes and chamaephytes are distinctly represented in areas with very low rainfall (150 - 400 mm annual rainfall) and remain constant at higher rainfall figures. Hemicryptophytes and geophytes increase along the rainfall gradient and therophytes show an optimum between 200 and 500 mm of precipitation. The correlation of life forms and mean annual temperature is less clear, though hemicryptophytes and geophytes show a negative correlation with mean annual temperature and mean annual minimum temperature. Evenari et al. (1975) suggested that ephemerism and persistence represent two major strategies of resisting the dry season. The persistent plants are 'arido-active' owing to the fact that they maintain their assimilating and transpiring organs throughout the whole summer, whereas ephemeral plants are 'arido-passive', i.e. they occur only directly after precipitation events. Among the persistent plants the chamaephytes are better adapted to drought than the phanerophytes, since they partly reduce their transpiring and assimilating organs during the dry summer (Orshan 1964, Orshan & Sand 1962). Among the ephemeral plants therophytes are more resistant to 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.

According to Danin and Orshan's results the predominance of chamaephytes in the northern Richtersveld is due to the low precipitation values with approx. 100 mm mean annual precipitation. The insignificant evidence of hemicryptophytes and geophytes within the eastern Gariep can be put down to the fact that the precipitation values decrease and the temperature increases from the coast to the interior (see chapter 1.2.1.). According to Orshan and Sand the lower occurrence of phanerophytes unlike the chamaephytes can be seen in their poorer adaptation to drought. The relatively high amount of therophytes in contrast to the hemicryptophytes and geophytes reflects the

better adaptation of seeds to drought.

The life form spectrum of the Hester Malan Nature Reserve near Springbok in Namaqualand (Van Rooyen et al. 1990) reflects the results for the northern Richtersveld: high values for chamaephytes, geophytes and therophytes and low percentage values for phanerophytes and to a lesser extent for hemicryptophytes.

Additionally the abundance of succulents correlates with the occurrence of frost (Werger 1986) owing to the fact that succulents can be damaged easily by frosts (Larcher et al. 1973). But it is also correlated with a dry climate where drought periods are regularly interrupted (Werger 1986). Both points can be seen in the coastal, winter rain driven, semi-desert of the Richtersveld with moderate temperature amplitudes.

*The life and growth form spectra of the northern Richtersveld in comparison with other deserts*

As the plant functional types such as the life and growth form of species mirror the influencing environmental factors they help to increase the ecological understanding (Floret et al. 1989, Duckworth 2000). Otherwise a classification on the basis of growth forms is useful in characterising vegetation at a coarser level than the taxonomic, which gives the opportunity to compare totally different floristic regions (Midgley & Heyden 1999).

Werger (1986) compared the life form spectra along a west-eastern transect corresponding to the climate gradient from the winter rainfall via the uniform to the summer rainfall zone. The decreasing amount of chamaephytes from the winter rainfall zone (32 % at the Hester Malan Nature Reserve near the coast) to the summer rainfall zone (14 % at the Southern Kalahari) is obvious as is the increasing amount of phanerophytes over the same section (4 % to 12 %).

The same situation is true for the northern Richtersveld where the continuous changes of the life form spectra is given in a confined space.

Changes in the life form spectra are revealed along a north-south transect from seasonal winter rainfall to unpredictable summer rainfall, which fails for years. The Kaokoland in Namibia with annual precipitation of about 20 to 200 mm (Schulte 2002) and the Namib Desert with annual precipitation values of 15 to 100 mm (Hachfeld 1996) reveal similar life form spectra among each other, but show differences to the Richtersveld. The life form occurrence of geophytes, hemicryptophytes and nanophanerophytes are comparable whereas the dominating life forms are different (Fig. 4.3). Within the Kaokoland and the Namib Desert the therophytes predominate whereas in the Richtersveld the chamaephytes are the dominating life form. The reason for this difference may be explained by the fact that therophytes are the best adapted life form to drought and unpredictable precipitation closely followed by chamaephytes (Orshan 1964, Orshan & Sand 1962). It has to be mentioned that Schulte (2002) established for the dry Savanna vegetation of the Kaokoland, a shift of hemicryptophytic to annual

grasses determined by the grazing impact. The increased therophytes in the Kaokoland are therefore not only induced by climatic conditions.

The winter rain driven Israeli deserts with mean annual precipitation values of 135 mm (Danin & Orshan 1990) show similar life form spectra such as in the Central Namib Desert. The therophytes dominate the spectrum followed by chamaephytes. Geophytes and hemicryptophytes reach low values within the spectrum (Fig. 4.3).

Esler et al. (1999) compared the Succulent Karoo with other winter-rainfall deserts in North America on the basis of plant structure and function. The comparison reveals unusual differences. The Succulent Karoo is unusual in its moderate winter temperatures and predictable rainfall, which has resulted in communities dominated by functionally similar dwarf succulent shrubs. The more continental, temperate climate of the North American deserts has lead to communities with a high diversity in vegetation structure.

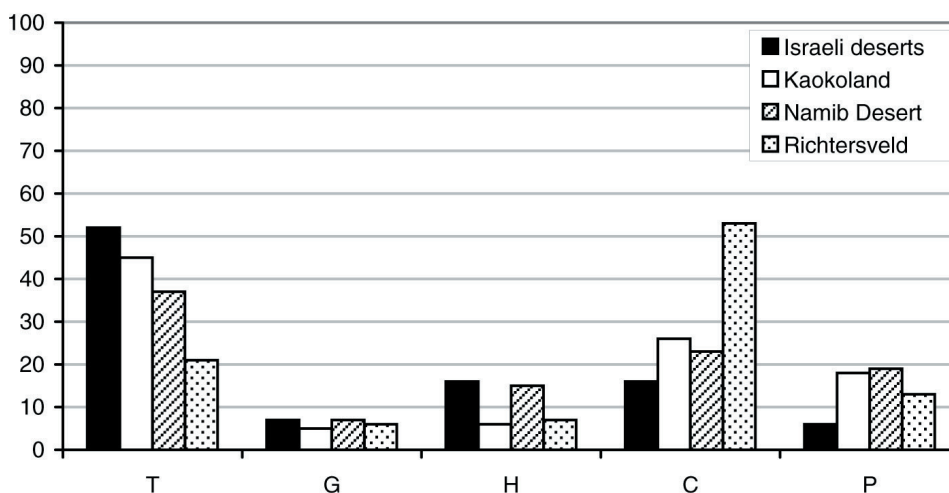


Fig. 4.3: Comparison of life form spectra of different study areas along the south-western coast and in NE Africa. G = geophytes, H = hemicryptophytes, C = chamaephytes; P = phanerophytes and T = therophytes.

*Life form and growth form spectra along an altitudinal gradient - the extra-zonal vegetation of the Fynbos*

The study of vegetation along an altitudinal gradient is the focus of recent worldwide interest by ecologists owing to the fact that the environmental control of vegetation patterns acts within a confined space. Investigations along altitudinal gradients were undertaken in Israel (Auerbach & Shmida 1993), in the Cape Floristic Region, South Africa (Linder et al. 1993) in south-west Saudi Arabia (Hegazy et al. 1998) and in the Atacama, Chile (Gutiérrez et al. 1998).

The detailed investigation of an altitudinal gradient on the escarpment of the southern Richtersveld (Van Zylsrus, Stinkfonteinberge) revealed high correlations between environmental factors and the distribution of life and growth forms (Schüttler 2002, masters thesis). The results strikingly reflect the situation of the strong elevation differences in the whole Richtersveld. Schüttler was able to establish a correlation of the factors substrate directly and climate indirectly with the growth form distribution. The climatic factors are positively correlated with the altitude.

The chamaephytes dominate on the footslopes followed by the phanerophytes, whereas the phanerophytes dominate on the mid-slopes and the amount of chamaephytes decreases. The high occurrence of hemicryptophytes on top of the escarpment is conspicuous where the dominant nanophanerophytes reach the highest value of abundance along the slope, followed by the chamaephytes.

The life and growth forms therophytes, geophytes, leaf succulent chamaephytes, pubescent and ericoid-leaved chamaephytes and bifacial-leaved nanophanerophytes are distributed throughout the whole slope. Bifacial-leaved chamaephytes and leaf succulent pachycaul nanophanerophytes are almost restricted to the foot and mid-slopes. The pachycaul growth form is interpreted as an adaptation to dry conditions on footslopes (Pavon et al. 2000). The same is true for the bifacial-leaved chamaephytes (Campbell & Werger 1988).

Leaf succulent pachycaul chamaephytes, hemicryptophytes and ericoid-leaved nanophanerophytes are almost restricted to the top of the slope. The hemicryptophytes indicates seasonal (Raunkiaer 1934) and high precipitation values, but also lower air temperatures (Danin & Orshan 1990) on the top. The increasing appearance of nanophanerophytes from the footslope to the top is correlated with the increasing precipitation value (Pavon et al. 2000, Danin & Orshan 1990).

Ericoid-leaved nanophanerophytes are a characteristic growth form for the dry Fynbos (Campbell 1985, 1986). The appearance of this growth form above 1000 m and the occurrence of ericoid Asteraceae indicates Fynbos elements for the Richtersveld. The appearance of leptophylls, elytropappoids, pubescent shrubs and perennial grasses with high cover percentage could also indicate the occurrence of Renoster Shrubland, which is a non-fynbos vegetation type of the Fynbos biome (Campbell 1985).

The pH-value of the soil decreases from the footslope to the top of the Van Zylsrus mountain, and has been established for the whole Richtersveld (Fig. CCA soil). The electronic conductivity as well as the nutrients increase from the footslope to the mid-slope and decrease again to the top. The appearance of the Fynbos elements corresponds to the decrease of the nutrients.

The Fynbos structure of small-leaved sclerophyllous was interpreted to be a response to the low soil nutrient levels (Cowling & Campbell 1983, Campbell & Werger 1988). The distinction of Fynbos and karroid and grassy non-Fynbos vegetation types is linked

to the soil chemistry and to a rainfall and leaching gradient (Campbell 1986). The Fynbos occurs on nutrient poor soils with low pH-value owing to higher rainfall and leaching processes.

So it could be expected that the altitudinal change of the life and growth forms on the Van Zysrus mountain correspond with the altitudinal gradients of precipitation and temperature as well as with the different soil conditions at the foot, mid-slopes and the top respectively.

The appearance of Fynbos elements on the escarpment of the semi-arid Richtersveld is comparable to the harbouring of karroid vegetation elements and elements of highland Savanna on the inselbergs of the Central Namib. Both features follow the principle of habitat constancy and could be interpreted as elements of a once widespread flora that became fragmented as the climate changed and then evolved further in isolation (Adamson 1958).

In conclusion it can be mentioned, that the analysis and classification of vegetation on life and growth form levels is advantageous when comparing vegetation types on a biome scale. Totally different floristic vegetation types can be compared with respect to their determinants, which could be e.g. climatical or edaphical factors.

The life form chamaephytes and the growth form leaf succulence dominate the vegetation of the Succulent Karoo within the Richtersveld. To the east, following a climatic gradient, the phanerophytes and stem succulence increase, which indicates the transition to the Nama Karoo. The predominance of chamaephytes is mainly caused by the low precipitation values with approx. 100 mm. The chamaephytes are better adapted to drought conditions than the phanerophytes. The dominance of functionally similar succulent dwarf shrubs is also a result of moderate winter temperatures and predictable rainfall. Even though the winter rainfall driven deserts of North America show comparable mean precipitation values per year, the more continental, temperate climatic conditions causes, in contrast, more diverse vegetation structures.

The comparison of life form spectra from the southern Namib (Richtersveld) to other vegetation types showed differences in the predominating species. In Kaokoland, Central Namib and the Israeli deserts the therophytes, and not the chamaephytes, dominate the life form spectra. The reason for these differences could also be found in the moderate temperatures and the predictable rainfall of the southern Namib that is neither true for the summer rainfall driven Central Namib and Kaokoland nor for the Israeli winter rainfall deserts. These moderate temperatures are caused by the frequent fog and winter rain clouds that reduce the daily saturation and the cooling during the night. The fog also occurs in Central Namib but there the area of occurring fog is restricted to a narrow strip along the coast. The dominating therophytes in the more arid regions are optimally adapted to the unpredictable rains owing to the fact that their seeds can germinate



directly after precipitation events.

The altitudinal change of life and growth forms on the Van Zysrus mountain corresponds to the altitudinal gradients of precipitation and temperature as well as to the different soil conditions at the foot, mid-slope and top respectively. Hemicryptophytes with the most occurrences on the top indicate seasonal and high precipitation. The increasing appearance of nanophanerophytes from the footslope to the top is also correlated with the increasing precipitation. The appearance of ericoid-leaved nanophanerophytes and ericoid Asteraceae on top of the escarpment indicates Fynbos elements for the semi-arid Richtersveld following the principle of habitat constancy.

The pH-value of the soil decreases from the footslope to the top whereas the electrical conductivity and the nutrients increase from the footslope to mid-slope and decrease again from mid-slope to the top. Fynbos occurs on nutrient-poor soils with a low pH-value owing to higher rainfall and leaching processes.

#### **4.4. Digression: Reflections on degradation and the conflict of land use in the Richtersveld**

After a series of droughts, especially that of 1919, dried up rivers and water holes, over grazing and erosion were recognised in the eastern Karoo (Hoffman et al. 1999). These observations initiated the debate on desertification in South Africa. The negative changes in the Karoo landscape and agricultural productivity have only been attributed to agricultural impacts. The government of South Africa reacted with state agricultural initiatives such as the 'Stock Reduction Scheme' (Pringle et al. 1982), privatisation of Karoo communal lands (Boonzaier et al. 1990) and the 'National Grazing Strategy' (Du Toit et al. 1991) to combat the degradation of the Karoo (Hoffman et al. 1999).

Many authors criticised the fact that despite the long discussion on desertification very little is known about the ecological processes and the history of the two main agricultural production systems in the Karoo, the communal and commercial system (e.g. Hoffman & Cowling 1990, Dean et al. 1995, Hoffman et al. 1999).

The commercial farms cover about 80 % of the Karoo. Only 2 - 3 % of the karroid rangeland is communally used, mainly in the western part in the 'Rural Coloured Reserves'. The main trend of vegetation changes on commercial farms in the eastern Karoo shows a recent shift from a perennial grass-dominated to an increasingly shrub-dominated vegetation with more annual grasses. Evidence for this trend was provided by the analysis of stable carbon isotopes in organic soil matter from eastern Karoo sites (Bond et al. 1994). Within the Succulent Karoo, on communally used land, the degradation can be seen through a shift from a perennial, leaf succulent shrub-land with e.g. *Ruschia* species to an annual-dominated vegetation often with an associated mix of unpalatable, e.g. *Chrysocoma ciliata*, or poisonous plants, e.g. *Galenia africana* or *Tylecodon wallichii*

(Hoffman et al. 1999). How these changes affect the ecological system and if it influences the biodiversity are not known.

In the nineties of the last century the debate on desertification followed a new direction. With increasing knowledge the term 'desertification' became a focus point. Desertification stands for inexorable desert dune expansion and is not inappropriate for the developments in the karroid vegetation (Dean et al. 1995). There has been no evidence for progressive irreversible Karoo degradation up until now. Observations in the southern Orange Free State have shown an opposite trend of vegetation changes than were postulated for the eastern Karoo: the grasses increased in the eighties (Hoffman & Cowling 1990). The higher summer rainfall during the year mentioned was responsible for this trend rather than the long-term summer rainfall mean. The authors suggest that perennial grasses may not have dominated the pre-colonial eastern Karoo and seasonal rainfall effects caused the vegetation changes. Pollen analysis by Bousman & Scott (1994) emphasized this hypothesis. The pollen evidence showed that the last major shift from grassland to Karoo shrub vegetation began before Europeans settled in the karroid landscape. Bousman and Scott assumed that rainfall fluctuations originally induced this vegetation change.

Even though evidence, which emphasizes the dominating control of climatic variations on the observed vegetation changes, has increased, the impact of grazing must also be taken seriously. The effect of grazing intensifies with increasing aridification and accelerates degradation and erosion processes as observed throughout the karroid vegetation and soils.

The communal areas situated in the western, more arid Succulent Karoo have not become a part of the South African's desertification debate, owing to its lower productivity. However, even now the capacity of the landscape is becoming exhausted. In Namaqualand the communal areas comprise 26 % of the land and are home to 45 % of the total population (Anon 1991). Additionally the livestock density is generally twice the recommended carrying capacity estimates (Hoffman et al. 1999). It is therefore expected that degradation in the Succulent Karoo is even higher than on private farms with a lower livestock density (Hoffman & Ashwell 2001). In addition, with the closing of the mines throughout the western coast the pressure on the Succulent Karoo landscape will increase over the next ten years (see chapter 1). A positive influence on the maintenance of the landscape is the transhumance movements of the indigenous Khoikhoi populations, which are still practiced today.

Probably more than 2000 years of a nomadic or semi-nomadic life-style prevail in the Richtersveld (Webley 1997). The mobile extensive system of stock farming with small animals such as goats and sheep enables a sustainable grazing exploitation in this semi-arid desert.

It has to be emphasized that the indigenous habitants, the *Nama*, have lived and

sustained themselves in this difficult and fragile environment showing respect for the land (Hendricks 1998). It is only to their credit that this extraordinary landscape still exists with its high species diversity and economic productivity.

The *Nama* are involved in the management of the park and have agreed to limit the total number of sheep and goats to 6600 animals. About 14 herds with an average size of 450 animals exist within the park (Hendricks 1998).

Even in this sustainable utilized landscape grazing and trampling effects on the vegetation and soil have been recorded. The management of the park requires more detailed observation and research on the problematic of grazing impact (Hendricks 1998, SANP 1996).

One part of the research project in the Richtersveld National Park that was installed in order to understand the degradation processes, deals with the spatial and temporal movement patterns of the animals and their diets (Hendricks 1998).

Gotzmann (2002) investigated in another part of the research project the vegetation dynamics in the Richtersveld with respect to the factors climate and grazing on permanent plots. She could prove that the climatic factors and especially the precipitation patterns mainly control the vegetation dynamics. The grazing also influences the vegetation in terms of trampling and feeding, which results in degradation and erosion processes. Comparable results were resolved for the arid vegetation of the Hoanib River catchments, NW-Namibia (Leggett et al. 2003). The vegetation changes depended rather on the annual rainfall than on the intensity of land use.

There is no evidence of regeneration processes on fenced plots where grazing was avoided. Hence, Gotzmann suggested that recovery of the semi-desert vegetation from grazing is a long-term process. The study period of seven years was not sufficient to detect the grazing effect. On experimentally disturbed plots Gotzmann established little regeneration of the vegetation. She assumed a regeneration period of 10 to 20 years after the disturbance until the vegetation reaches its previous state (see also Jürgens et al. 1997).

Some of the fenced permanent plots were installed in the vicinity of stock posts. Gotzmann recorded invader species on these plots. The number of invaders was the highest directly on the stock post and on over grazed pastures near the towns (Gotzmann 2002, Osterloh 2000). The penetration of invaders can be seen as a consequence of grazing and especially over grazing (Milton et al. 1999, Pettit et al. 1995). The results of Gotzmann and Osterloh are further highlighted by the observations that were made during the fieldwork concerned with the phytosociological analysis of this study for which a large area of the northern Richtersveld was investigated. A second indicator for grazing impact is the occurrence of spinescence. Milton (1991) recorded 10 % spinescent species in the Karoo vegetation. In the northern Richtersveld only eight of 622 species (1.3 %) show spinescence.

Osterloh (2000) examined the vegetation and soil properties on stock posts in the Richtersveld. The main results of her masters thesis are briefly summarized here. The influence of the grazing effect decreases with distance to the centre of the stock post where the animals are collected in a fenced kraal over night. The accumulation of faeces results in a decreasing amount of stone content within the stock post. The dark colour of the soils indicates an increasing amount of organic substrate. The analysis of the soil properties shows the same feature. The pH-value, the electronic conductivity and the amount of nutrient salt increases in the direction of the stock post centre. Trampling leads to a denser soil structure.

The centre of a stock post is mostly devoid of any vegetation cover. After the intensive exploitation a spontaneous colonization of ruderal vegetation take place (Osterloh 2000). The species composition differs totally from the non-disturbed vegetation in the surrounding area. In contrast to the zonal vegetation, which mainly depends on the climatic factors, the vegetation of the stock posts reveals dependence on edaphic conditions and can therefore be regarded as azonal vegetation. The diversity index is lower than within the surrounding vegetation, but the canopy cover is mostly higher. It is assumed that the higher phosphate contents are responsible for this feature.

The life form spectra are different from the surrounding vegetation although the ruderal vegetation grows under the same climatic conditions. The pioneers consist of mainly leaf succulent therophytes, which are facultative perennials. The later succession stages are mainly formed by leaf succulent chamaephytes and nanophanerophytes.

During the fieldwork period of the study on hand (1996 - 1999) 32 stock posts were recorded within the park (see Fig. 4.4 for a map with stock post locations). About 25 % of these stock posts were occupied between July and September. The degradation around the stock posts is restricted to an area of about 10 to 200 m in diameter (Osterloh 2000). The extent of degraded vegetation is therefore not that high. However, it has to be mentioned that over 2000 years of grazing impact have certainly influenced the species composition and diversity and canopy cover of the zonal vegetation that surrounds the stock posts. Due to the high species diversity and the diffuse vegetation cover, which still exists within the Richtersveld, the impact of grazing on the zonal vegetation could be regarded as moderate.

The same is true for the stock posts, where the grazing impact leads to disturbance or directly to destruction of the vegetation. If the disturbance is restricted to locally small areas, then the stock posts can not be considered as a serious problem for the sustainable exploitation of this region and the maintenance of the floristic diversity (Osterloh 2000). On the contrary moderate exploitation promotes the habitat diversity and dynamic of a system, because restricted disturbance creates ecological niches for species of low competition strength (Wiegand et al. 1997). The high turnover rates of the chamaephytes under winter rainfall conditions can be put down to their short-term life

periods that make them less sensitive to disturbance (Jürgens et al. 1999). This is not true for the species in the summer rainfall region where rare precipitation events reduce the regeneration capacity.

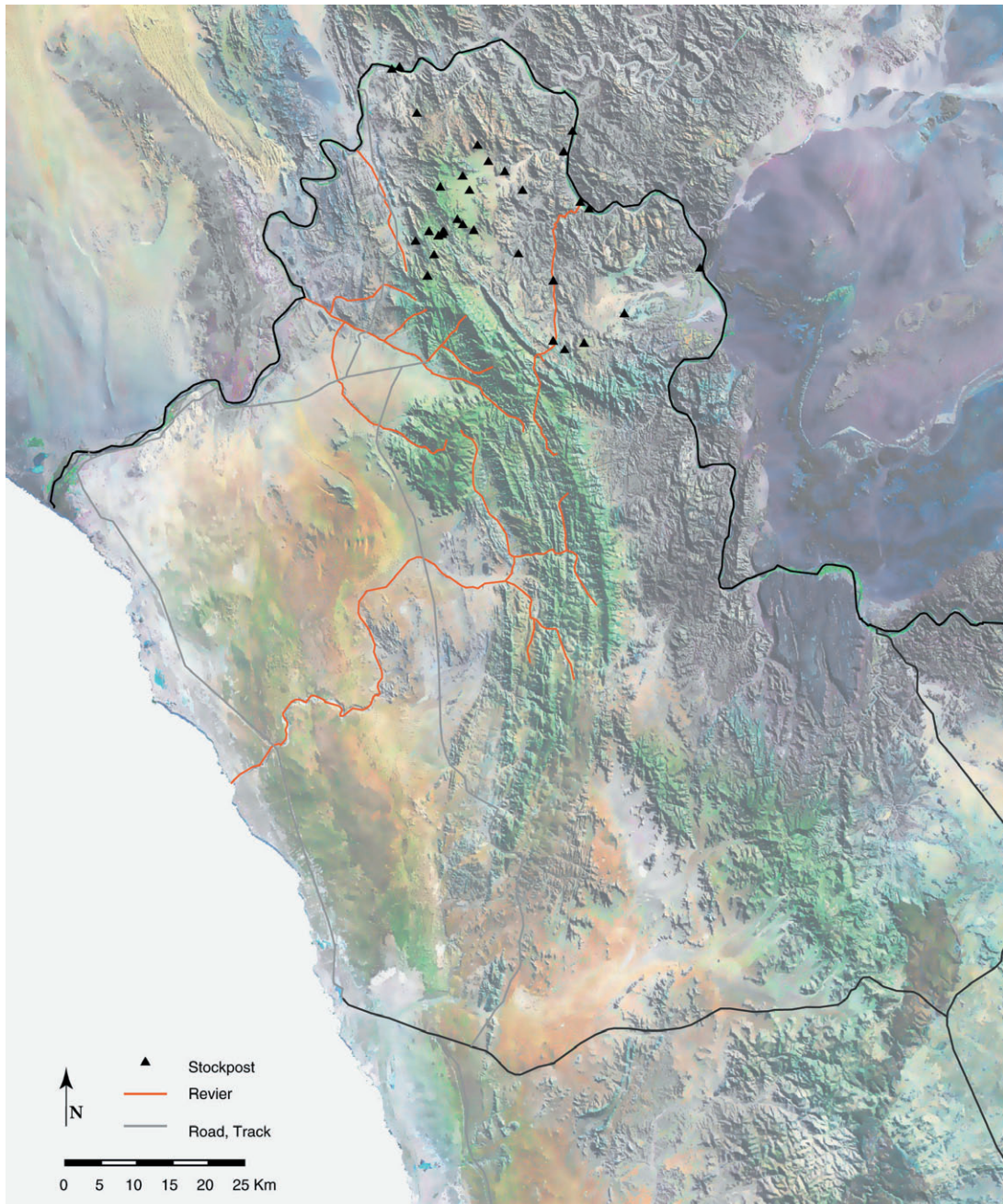


Fig. 4.4: Map of the northern Richtersveld showing the distribution of stock posts within the national park area as was noted during the field work.

*Present erosion versus accumulation processes*

Besides the reduction of vegetation cover and change in species composition as a result of browsing, trampling effects also disturb the vegetation and the soil surface. Erosion, for example, is a marked sign, which indicates the extent of disturbance. Gully erosion and absent vegetation indicate a high grazing impact, where the disturbance has already progressed. Early signs can be recognised by the appearance of phytogenic mounds or in the reduction of microbiotic crusts. A quantitative analysis enables the opportunity to estimate the rate of erosion. The results of this analysis, compiled for the Koeroegabvlakte within the Succulent Karoo, are briefly introduced and what should be discussed is, if this result is caused by climatic developments or by grazing impact.

Today the erosion processes prevail over the accumulation processes in the northern Richtersveld on the silty plains. This result is based on the fact that the phytogenic mounds counted prevail over the down axis (Fig. 3.9). The lowest value of phytogenic mounds and therefore of erosion processes, was observed in the upper part of the plain. This result correlates with the highest percentage of microbiotic or biological soil crusts.

Microbiotic crusts are assemblages of non-vascular plants and stabilize the soil against water and wind erosion, increasing landscape stability, particularly in areas of low vascular plant cover (Eldridge & Greene 1994, Belnap & Lange 2001). Microbiotic crusts play an important role in rangeland ecosystems above all in the ecologically sustainable development of arid and semi-arid grazing systems.

Physical crusts provide protection against erosion but are obviously not as effective as microbiotic crusts. The most phytogenic mounds were recorded where physical crusts prevail. The erosion processes are the highest on the footslope and at the end of the plain. The water run-off at these locations might be higher than in the middle part of the plain. The amount and speed of the rainwater and therefore the erosion potential is high when it enters the plain coming from the steeper slopes. The speed of the rainwater reduces whilst flooding the gently inclined plain. However, with further draining, the amount of water increases and reaches the highest value at the end of the plain and therefore the end of the drainage system. Hence, the erosion potential increases as well. The lower erosion potential of the water in the upper part of the plain might be the reason for the higher amount of microbiotic crusts. The increased movements of the surface on the footslopes and at the end of the plain probably prevent the development of the microbiotic crusts. The occurrence of microbiotic crusts also depends on other factors such as the availability of water and intensity of grazing. In arid and intensively grazed regions the appearance of microbiotic crusts is strongly reduced (Warren & Eldridge 2001).

Beside the limiting factors movement and water supply, grazing is also important in the Richtersveld. Goats intensively grazed the Domoroghvlakte near the Koeroegabvlakte in 1998. Deep erosion channels and gullies could be observed, beginning directly along the main trails of the animals (Photo A. P21). The animal hoofs destroyed the microbiotic crusts. A rest period of two years without grazing was sufficient for the regeneration of

this pasture. The channels were once again full of soil material and the vegetation cover was closed again, but the microbiotic crusts were still absent as they need a longer time to recover. Belnap & Eldridge (2001) calculated the estimated recovery times of dated disturbance of known severity in the Mojave, Sonoran, Chihuahuan and Colorado Plateau deserts of the western USA. In cold desert the recovery time is estimated to be about 14 (Cyanobacteria) to 875 years (other lichens) after removal, only 7 to 70 years after crushing. In hot deserts the recovery takes place more slowly 80 to 3700 years after removal and two to 90 years after crushing. The surface is abandoned to wind and water, until the microbiotic crusts once again develops between the plant individuals.

The occurrence of microbiotic crusts on sandy soils e.g. at the coast is more limited than on the silty habitats of the plains even though the impact of grazing has the same intensity (pers. observ., see also Stöcker 1998). Fine-textured soils generally support greater cover of a more diverse biological crust than coarse-textured soils (Belnap & Lange 2001) and the recovery of fine-textured soils is faster when compared to sandy soils (Belnap & Eldridge 2001).

In conclusion, the degradation of the Succulent Karoo vegetation in the Richtersveld National Park is still to be regarded as moderate. The amount and spatial expansion of the stock posts has been relatively low up until now and increases, more than reduces, the habitat diversity of the matrix vegetation. The vegetation of the fenced permanent plots showed no significant changes after the observation period of seven years (Gotzmann 2002). Climatic factors were regarded as the dominant controllers of the vegetation dynamics in comparison to the grazing impact. Indicators of over grazing such as the increasing appearance of invaders and spinescent species are not seen to be critical.

However, future developments could change the sustainable exploitation. Within the younger *Nama* herders a change of moral concept has appeared (see chapter 1.). The flock has increasingly become an object of prestige, which leads to an increasing number of animals per stock (pers. comm. H. Hendricks 1997). The contractual allowed maximum of 6600 grazing units has recently been exceeded and the reduction back to this limit proceeds only slowly (pers. comm. P. Gordon 1999, pers. comm. H. Hendricks 1999). The erosion processes, which prevail, will be strengthened with increasing stock numbers, which leads to more grazing and trampling effects. The results can already be observed outside the park around the villages Khubus (Annisvlakte) and Eksteenfontein, where the leaf succulent dwarf shrubs have been replaced by therophytes. Only the unpalatable species such as *Euphorbia*-species (e.g. *E. gummifera*) have remained. Increasing numbers of tourists and the expected closure of the diamond mines along the coast over the next ten years has increased the pressure on the landscape and forms additional problems for the future development of the northern Richtersveld.

The maximum number of 6600 grazing units, which is based on the 'Carrying Capacity Concept', is not flexible enough to react to climatic variabilities within a semi-arid landscape. Maybe this is one point that has to be changed. An intensification of the

monitoring projects is desirable. Monitoring on the basis of remote sensing may also be a useful tool for detecting degradation (Worcester & Dalsted 1979). However it is to be expected that it will only be able to be usefully employed on the plain surfaces for example along the coastal plain, as was shown for the Southern Kalahari (Belnap & Gillette 1998). Nevertheless it is more important to detect the first signs of degeneration processes such as changes in the species composition or the reduction of microbiotic crusts to enable a direct reaction. If the degradation could be detected on the scale of remote sensing data then the processes could be exceeded to a point of no return. Therefore the tool of remote sensing could only supplement and not replace the monitoring of vegetation dynamics on permanent plots or the monitoring of the movements of the herds and their diet.

The most important structure that has to be maintained is the teamwork of the National Parks Board and the *Nama*, which is already installed in the national park's contract. The structure of this management plan should be able to resolve the problems in future years. The aim of the conservation issues can only be transposed successfully with respect for the culture of the *Nama* people.



## 5. Conclusion

The southern Namib is a semi-desert with precipitation well below 150 mm per year. In spite of its limited exploitation potential, in terms of water resource and high relief energy, the Richtersveld is the focus of a serious conflict of interests. The communal farmers require extensive land for their semi-nomadic economy. Due to decreasing profits along the coastal line the diamond mines have expanded along the Orange River valley into the national park area. The national park is attempting to combine the maintenance of the traditional life-style and culture of the *Nama* people as well as the conservation of the landscape in an unspoilt condition. Secondly the management of the park has opened up the landscape of exceptional beauty, in terms of biological and geological diversity, to a gentle ecotourism.

All these exploitation interests influence and, in future, will increasingly influence the ecosystem and therefore the vegetation cover. In this context there is an urgent demand for scientific research to document the present state of the ecosystem. By order of the management committee of the National Parks Board, several research projects have been initiated.

The study on hand set up a phytosociological classification for the northern Richtersveld on the basis of more than 800 vegetation relevés, and determines the environmental factors, which control the vegetation patterns. Therefore the factors climate, relief, and soil were established according to their significance as a controlling force. The results are presented in a detailed but preliminary vegetation map. The transition of the two floristic kingdoms, *Greater Cape Flora* and *Palaeotropis* is discussed on the basis of the phytosociological subdivision supplement of the life form distribution along the climatic gradient.

Five basic landscape units subdivide the vegetation into the predominating dwarf shrub communities on the coastal sand plain and silty plains and slopes of the escarpment; the dry shrub communities on silty slopes of the eastern Gariep; and the open shrub communities on gravelly flood plains and drainage lines. The detailed division reveals 23 associations, within four alliances of the Succulent Karoo (*Greater Cape Flora*) and three alliances of the Nama Karoo (*Palaeotropis*).

The climate variables, such as precipitation in winter and maximum air temperature in summer, are the main determining factors and predominate the factor soil on a regional scale. Acidity, carbonate and stone content as well as soil texture are the main soil properties that subdivide the vegetation communities on the plains. The mineral content and weathering composition of different geological units influences the vegetation indirectly via soil properties and by structuring the habitats. On a local scale relief was determined as the controlling factor. The north-south expositions of the slopes show obvious differences in vegetation cover and species composition.

The precipitation amount, with the lowest values at the Atlantic Ocean, increases with

the ascent of the African plate, reaching the highest values at the top and decreases gently down to the Orange River valley. The mean maximum air temperature is negatively correlated with the precipitation.

Along this climatic gradient the vegetation patterns change from a winter rainfall bordering on a summer rainfall regime. Those of the Nama Karoo replace the syntaxa of the Succulent Karoo. Species diversity and vegetation cover generally decreases with the exception of the escarpment where the highest abundance and species diversity were observed. The Orange River valley is interpreted as a minimum zone between the two climate regimes in terms of precipitation, species diversity and canopy cover. Abundance and cover increases again further east with the increasing influence of the summer rainfall regime.

Chamaephytes and leaf succulents dominate the vegetation of the Succulent Karoo within the Richtersveld. The predominance of leaf succulent dwarf shrubs correlates with low precipitation values and moderate temperatures at the coast. The occurrence of phanerophytes and stem-succulents increases, to the east, following the climatic gradient, which indicates the transition to the Nama Karoo. The relatively high occurrence of therophytes indicates the close vicinity to the desert, located further north (Central Namib Desert).

#### *Evaluation and outlook*

The rare occurrences of invader and spinescent species within the Richtersveld flora indicate moderate degradation within the park where it is locally restricted to the stock posts and their surroundings. Therefore the semi-nomadic pastoralism is to be seen as, an economy well adapted to annual vegetation variation with a sustainable land use. Degradation resulting in destruction could be observed around the villages Khubus, Eksteenfontein and Steinkopf, where the density of stock is high during the whole year. Intensive grazing enhances the dominating erosion processes under recent climatic conditions. However, the destruction caused by diamond mining has to be considered as more critical.

The pressure on the land will increase with the closure of the mines, which means the return of unemployed mine workers to their traditional form of pastoralism and with the change of the moral concept, which considers the herd as a prestige object. In spite of a sustainable land use by pastoralism the exploitation potential has reached its limit within the Richtersveld landscape due to restricted water resources. The resulting increase of stock units and a retirement of the transhumance concept would negatively influence the ecosystem and probably destroy its stable state.

The future monitoring of the ecosystem is of high importance. It uncovers degradation processes at an early stage and provides the opportunity to take direct reaction. The ongoing of the already installed research projects is undeniable. As well as the monitoring of the vegetation dynamics and the impact of grazing on the vegetation cover plus

the monitoring of the livestock dynamics and the impact of livestock on the vegetation. Furthermore the monitoring of vegetation changes on a regional scale would supplement the detailed observations. This research could be supported by a Geographic Information System (GIS) based on the results, which have arisen from this study with the detailed vegetation map.

The degradation within the park is moderate thanks to the management committee composed of local people and members of the National Parks Board. The continuation of the national park with a strict management and its extension into the south (Namaqualand) would be desirable.



## 6. References

- Abrams, M. M., P. J. Jacobson, K. M. Jacobson, and M. K. Seely. 1997. Survey of soil chemical properties across a landscape in the Namib Desert. *Journal of Arid Environments* 35:29-38.
- Acocks, J. P. H. 1953. Veld types of South Africa. *Mem. Bot. Surv. S. Afr.* 28:1-192.
- Adamson, R. S. 1958. The Cape as an ancient African flora. *Pres. Add. Sect. K. (Botany), Adv. Sci.* 15:118-127.
- AG-Bodenkunde. 1994. *Bodenkundliche Kartieranleitung*, 4 edition. E. Schweizerbart'sche Verlagsbuchhandlung, Hannover.
- Andersen, M. C., and F. R. Kay. 1999. Banner-tailed kangaroo rat burrow mounds and desert grassland habitats. *Journal of Arid Environments* 41:147-160.
- Anon, C. 1991. *Agricultural development programme: Karoo region*. Department of Agricultural Development, Pretoria.
- Arnold, T. H., and B. de Wet. 1993. Plants of southern Africa: Names and distribution. *Mem. Bot. Surv. S. Afr.* 62:1-825.
- Auerbach, M., and A. Shmida. 1993. Vegetation change along an altitudinal gradient on Mt Hermon, Israel - no evidence for discrete communities. *Journal of Ecology* 81:25-33.
- Barkman, J. J. 1988. New system of plant growth forms and phenological plant types. Pages 9-44 in M. J. A. Werger, editor. *Plant form and vegetation structure*, The Hague.
- Beals, E. W. 1984. Bray-Curtis ordination: an effective strategy for analysis of multivariate ecological data. *Advances in Ecological Research* 14:1-55.
- Beaumont, P., B., G. H. Miller, and J. C. Vogel. 1992. Contemplating old clues to the impact of future greenhouse climates in South Africa. *South African Journal of Science* 88:490-498.
- Becker, T., and N. Jürgens. 2000. Vegetation along climate gradients in Kaokoland, North-West Namibia. *Phytocoenologia* 30:543-565.
- Belnap, J. 2001. Biological soil crusts and wind erosion. Pages 339-347 in J. Belnap and O. L. Lange, editors. *Biological soil crusts: structure, function, and management*. Springer-Verlag, Berlin, Heidelberg, New York.
- Belnap, J., and D. Eldridge. 2001. Disturbance and recovery of biological soil crust. Pages 363-383 in J. Belnap and O. L. Lange, editors. *Biological soil crusts: structure, function, and management*. Springer-Verlag, Berlin, Heidelberg, New York.
- Belnap, J., and D. A. Gillette. 1997. Disturbance of biological soil crusts: impacts on potential wind erodibility of sandy desert soils in south-eastern Utah. *Land. Degrad. Dev.* 8:355-362.
- Belnap, J., and O. L. Lange. 2001. Structure and functioning of biological soil crusts:

- a synthesis. Pages 472-479 in J. Belnap and O. L. Lange, editors. *Biological soil crusts: structure, function, and management*. Springer-Verlag, Berlin, Heidelberg, New York.
- Belnap, J., R. Prasse, and K. T. Harper. 2001. Influence of biological soil crusts on soil environments and vascular plants. Pages 282-300 in J. Belnap and O. L. Lange, editors. *Biological soil crusts: structure, function, and management*. Springer-Verlag, Berlin, Heidelberg, New York.
- Berzborn, S. 2001. Vernetzung wirtschaftlicher und sozialer Strukturen: Landbesitz und Haushaltsökonomie im Übergangsbereich vom Sommer- zum Winterregen, Südliche Namib. Ergebnisbericht des SFB 389 Universität zu Köln.
- Berzborn, S. 2002. "Ek is 'n Nama, want ek praat die taal". The Richtersveld and the national language policy in South Africa. in T. Hohmann, editor. *The San and the State*. Rüdiger Köppe, Köln.
- Besler, H. 1992. *Geomorphologie der ariden Gebiete*. Wiss. Buchges., Wiesbaden.
- Boenigk, J. 1998. Vegetations- und bodenkundliche Untersuchungen von Viehposten im Richtersveld/Republik Südafrika unter Verwendung neuer bodenanalytischer Verfahren. Unveröff. Diplomarbeit, Universität zu Köln.
- Bolus, H. 1875. Letter from Mr. Bolus to Dr. J. B. Hooker. *Journal of the Linnean Society* 14:482-484.
- Bolus, H. 1886. *Sketch of the flora of South Africa*. Richards, Cape Town.
- Bolus, H. 1905. *Sketch of the floral regions of South Africa*. Maskew Miller, Cape Town.
- Bond, W. J., W. D. Stock, and M. T. Hoffman. 1994. Has the Karoo spread? A test for desertification using carbon isotopes from soils. *South African Journal of Science* 90:391-397.
- Bornkamm, R. 1990. The plant communities of the Western Desert of Egypt. *Phytocoenologia* 19:149-231.
- Bousman, B., and L. Scott. 1994. Climate or overgrazing? The palynological evidence for vegetation change in the eastern Karoo. *South African Journal of Science* 90:575-578.
- Bousman, C. G., T. C. Partridge, L. Scott, S. E. Metcalfe, J. C. Vogel, M. Seaman, and J. S. Brink. 1988. Palaeoenvironmental implications of Late Pleistocene and Holocene valley fills in Blydefontein basin, Noupoot, C. P., South Africa. *Palaeoecology of Africa* 19:43-67.
- Brain, C. K., and V. Brain. 1977. Microfaunal remains from Mirabib: Some evidence of palaeo-ecological changes in the Namib. *Madoqua* 10:285-293.
- Braun-Blanquet, J. 1928. *Pflanzensoziologie - Grundzüge der Vegetationskunde*. Springer-Verlag, Berlin.
- Braun-Blanquet, J. 1951a. *Pflanzensoziologie. Grundzüge der Vegetationskunde*. Springer-Verlag, Wien.

- Braun-Blanquet, J. 1951b. Pflanzensoziologische Einheiten und ihre Klassifizierung. *Vegetatio* 3:126-133.
- Braun-Blanquet, J. 1955. Zur Systematik der Pflanzengesellschaften. *Mitt. Florist.-Soziol. Arbeitsgem. N. F.* 5:151-154.
- Brink, J., and L. Webley. 1996. Faunal evidence for pastoralist settlement at Jakkalsberg, Richtersveld, Northern Cape Province. *Southern African Field Archaeology* 5:70-78.
- Bruckmann, C. 1997. Zur Kenntnis der Gattung *Drosanthemum* (Aizoaceae): Untersuchungen an Früchten und Blüten. Hamburg.
- Brummit, R. K. 1992. Vascular plant families and genera. Royal Botanic Gardens, Kew.
- Burke, A. 2001. Classification and ordination of plant communities of the Naukluft Mountains, Namibia. *Journal of Vegetation Science* 12:53-60.
- Burke, A. 2002. Plant communities of a Central Namib inselberg landscape. *Journal of Vegetation Science* 13:483-492.
- Burke, A. 2002. Properties of soil pockets on arid Nama Karoo inselbergs - the effect of geology and derived landforms. *Journal of Arid Environments* 50:219-234.
- Campbell, B. M. 1985. A classification of the mountain vegetation of the Fynbos Biome. Botanical Research Institute, Pretoria.
- Campbell, B. M. 1986. Montane plant communities of the Fynbos Biome. *Vegetatio* 66:3-16.
- Campbell, B. M., and M. J. A. Werger. 1988. Plant form in the mountains of the Cape, South Africa. *Journal of Ecology* 76:637-653.
- Cowling, R. M., and B. M. Campbell. 1983. A comparison of Fynbos and non-fynbos coenocline in the lower Gamtoos River Valley, southeastern Cape, South Africa. *Vegetatio* 53:161-178.
- Cowling, R. M., K. J. Esler, G. F. Midgley, and M. A. Honig. 1994. Plant functional diversity, species diversity and climate in arid and semi-arid southern Africa. *Journal of Arid Environments* 27:141-158.
- Cowling, R. M., G. E. Gibbs Russell, M. T. Hoffman, and C. Hilton-Taylor. 1989. Patterns of plant species diversity in southern Africa. Pages 19-50 in B. J. Huntley, editor. *Biotic diversity in southern Africa: Concepts and conservation*. Oxford Univ. Press, Cape Town.
- Cowling, R. M., and C. Hilton-Taylor. 1994. Patterns of plant diversity and endemism in southern Africa: an overview. Pages 31-52 in B. J. Huntley, editor. *Botanical Diversity in southern Africa*. NBI, Pretoria.
- Cowling, R. M., and C. Hilton-Taylor. 1997. Phytogeography, flora and endemism. Pages 43-61 in R. M. Cowling, D. M. Richardson, and S. M. Pierce, editors. *Vegetation of Southern Africa*. Cambridge Univ. Press.

- Cowlshaw, G., and J. G. Davies. 1997. Flora of the Pro-Namib Desert Swakop River catchment, Namibia: community classification and implications for desert vegetation sampling. *Journal of Arid Environments* 36:271-290.
- Cox, G. W. 1984. The distribution and origin of Mima mound grassland in San Diego County, California. *Ecology* 65:1397-1405.
- Cox, G. W. 1990. Soil mining by pocket gopher along topographic gradients in Mima moundfield. *Ecology* 71:837-843.
- Cramer, W. P., and R. Leemans. 1999. Global 30-Year mean monthly climatology, 1930 - 1960, V. 2.1. Available on-line [<http://www.daac.ornl.gov>] from Oak Ridge National Distributed Active Archive Center, Oak Ridge, Tennessee, USA.
- Danin, A., and G. Orshan. 1990. The distribution of Raunkiaer life forms in Israel in relation to environment. *Journal of Vegetation Science* 1:41-48.
- Dean, W. R. J., M. T. Hoffman, M. E. Meadows, and S. J. Milton. 1995. Desertification in the semi-arid Karoo, South Africa: review and reassessment. *Journal of Arid Environments* 30:247-264.
- Dierschke, H. 1994. The Braun-Blanquet approach to phytosociology as a basis for nature conservation, exemplified by montane grassland areas. Pages 1-9 in Y. Song, H. Dierschke, and X. Wang, editors. *Applied Vegetation Ecology - Proc. 35th Symp. IAVS*. East China Normal Univ. Press, Shanghai.
- Dierschke, H. 1994. *Pflanzensoziologie - Grundlagen und Methoden*. Ulmer Verlag, Stuttgart.
- Du Toit, P. C. V., C. D. Blom, and W. F. Immelman. 1995. Diet selection by sheep and goats in the Arid Karoo. *African Journal of Range and Forage Science* 12:16-26.
- Duckworth, J. C., M. Kent, and P. M. Ramsay. 2000. Plant functional types: an alternative to taxonomic plant community description in biogeography? *Progress in Physical Geography* 24:515-542.
- Eckhardt, N., N. Rooyen van, and G. J. Bredenkamp. 1995. The grassland communities of the slopes and plains of the north-eastern Orange Free State. *Phytocoenologia* 25(1):1-21.
- Eldridge, D. J., and R. S. B. Greene. 1994. Microbiotic soil crusts: A review of their roles in soil and ecological processes in the rangelands of Australia. *Aust.J.Soil Res.*
- Ellenberg, H. 1956. *Grundlagen der Vegetationsgliederung, Band 4, Teil 1: Aufgaben und Methoden der Vegetationskunde*. Pages 1-136 in *Einführung in die Phytologie* (H. Walter). Eugen Ulmer Verlag, Stuttgart.
- Ellenberg, H. 1981. Ursachen des Vorkommens und Fehlens von Sukkulente in den Trockengebieten der Erde. *Flora* 171:114-169.
- Ellenberg, H., and D. Müller-Dombois. 1967. A key to Raunkiaer plant life forms with



- revised subdivisions. Ber. geobot. Inst. ETH, Stifftg. Rübel, Zürich 37:56-73.
- Engler, A. 1882. Versuch einer Entwicklungsgeschichte der Pflanzenwelt insbesondere der Florengebiete seit der Tertiärperiode. Engelmann-Verlag, Leipzig.
- Esler, K. J., and R. M. Cowling. 1995. The comparison of selected life-history characteristics of Mesembryanthema species occurring on and off Mima-like mounds (*heuweltjies*) in semi arid southern Africa. Vegetatio 116:41-50.
- Esler, K. J., and P. W. Rundel. 1999. Comparative patterns of phenology and growth form diversity in two winter rainfall deserts: the Succulent Karoo and Mojave Desert ecosystems. Plant Ecology 142:97-104.
- Evenari, M., E.-D. Schulze, L. Kappen, U. Buschbom, and O. L. Lange. 1975. Adaptive mechanisms in desert plants. Pages 111-129 in F. J. Vernberg, editor. Physiological adaptation to the environment. Intext Educational Publishers.
- FAO-UNESCO. 1989. Soil map of the world. UNESCO, Isric, Wageningen.
- Floret, C., M. J. Galan, E. LeFloch, G. Orshan, and F. Romane. 1990. Growth forms and phenomorphology traits along an environmental gradient: tools for studying vegetation? Journal of Vegetation Science 1:71-80.
- Fuls, E. R., G. J. Bredenkamp, and N. v. Rooyen. 1992. Plant communities of the rocky outcrops of the northern Orange Free State, South Africa. Vegetatio 103:79-92.
- Gibbs Russell, G. E. 1987. Preliminary floristic analysis of the major biomes in southern Africa. Bothalia 17(2):213-227.
- Gibbs Russell, G. E., C. Reid, J. v. Rooy, and L. Smook. 1985. List of species of Southern African plants. Edition 2: Recent literature and synonyms. Part 1: Cryptogams, gymnosperms, monocotyledons. Mem.Bot.Surv.S.Afr. 51: 1-152.
- Gibbs Russell, G. E., L. Watson, M. Koekemoer, L. Smook, N. P. Barker, H. M. Anderson, and M. J. Dallwitz. 1990. Grasses of southern Africa. National Botanic Gardens/Botanical Research Institute, Pretoria.
- Giess, W. 1971. A preliminary vegetation map of South West Africa. Dinteria 4: 1-114.
- Giess, W. 1981. Die in der zentralen Namib von Südwestafrika/Namibia festgestellten Pflanzenarten und ihre Biotope. Dinteria 15:13-71.
- Goldblatt, P. 1978. An analysis of the flora of southern Africa: Its characteristics, relationships, and origins. Ann.Missouri Bot.Gard. 65:369-436.
- Good, R. 1974. The geography of the Flowering Plants, 4th edition. Longmans, London.
- Goodall, D. W. 1954. Objective methods for the classification of vegetation. III. An essay in the use of factor analysis. Australian Journal of Botany 2:304-324.

- Gotzmann, I. 2002. Vegetationsökologie und Vegetationsdynamik im Richtersveld (Republik Südafrika). Doktorarbeit, Universität Köln.
- Gutiérrez, J. R., F. López-Cortés, and P. A. Marquet. 1998. Vegetation in an altitudinal gradient along the Río Loa in the Atacama Desert of northern Chile. *Journal of Arid Environments* 40:383-399.
- Hachfeld, B. 1996. Vegetationsökologische Transektanalyse in der nördlichen Zentralen Namib. Unveröff. Diplomarbeit, Universität Hamburg.
- Hachfeld, B., and N. Jürgens. 2000. Climate patterns and their impact on the vegetation in a fog driven desert: The Central Namib Desert in Namibia. *Phytocoenologia* 30:567-589.
- Hammer, S. A. 1993. The genus *Conophytum*. A conograph. Succulent Plant Publications, Pretoria.
- Harmse, M. 1978. Schematic soil map of southern Africa south of latitude 16°30'S. in M. J. A. Werger, editor. *Biogeography and ecology of southern Africa*. Dr W. Junk bv Publishers, The Hague.
- Hartmann, H. E. K. 1984. Monographien der Subtribus Leipoldtiinae. VI. Monographie der Gattung *Jordaaniella* (Mesembryanthemaceae). *Bot.Jahrb.Syst.* 104(3):321-360.
- Hartmann, H. E. K. 1988. Monographien der Subtribus Leipoldtiinae. VIII. Monographie der Gattung *Cephalophyllum* (Mesembryanthemaceae). *Mitt.Inst.Allg.Bot.Hamburg* 22:93-187.
- Hartmann, H. E. K. 1998. New combinations in *Antimima* (Ruschioideae, Aizoaceae) from southern Africa. *Bothalia* 28:67-82.
- Hartmann, H. E. K. 1998. New combinations in Ruschioideae, based on studies in *Ruschia* (Aizoaceae). *Bradleya* 16:44-91.
- Hartmann, H. E. K., editor. 2002. *Illustrated handbook of succulent plants - Aizoaceae A-E, F-Z*. Springer-Verlag, Berlin-Heidelberg.
- Hartmann, H. E. K., and M. Dehn. 1987. Monographien der Leipoldtiinae. VII. Monographie der Gattung *Cheiridopsis* (Mesembryanthemaceae). *Bot.Jahrb.Syst.* 108(4):567-663.
- Hartmann, H. E. K., and S. Rust. 1994. Monographien der Leipoldtiinae. IX. Monographie der Gattung *Leipoldtia* L.Bolus s.lat. (Aizoaceae). *Verh.naturwiss.Ver.Hamburg (NF)* 34:275-351.
- Hartmann, H. E. K., and D. Stüber. 1993. Studies on the *Mesembryanthema* (Aizoaceae): On the spiny *Mesembryanthema* and the genus *Eberlanzia* (Aizoaceae). *Contrib. Bolus Herbarium* 15:1-75.
- Hegazy, A. K., M. A. El-Demerdash, and H. A. Hosni. 1998. Vegetation, species diversity and floristic relations along an altitudinal gradient in south-west Saudi Arabia. *Journal of Arid Environments* 38:3-13.
- Hendricks, H. 1998. Traditional stock farming in the Richtersveld. *Veld & Flora* 84: 86-87.

- Hennekens, S. 2000. Turbowin 1,98 h. Online-Publikation.
- Hill, M. O. 1973. Reciprocal averaging: an eigenvector method of ordination. *J. Ecol.* 63:237-249.
- Hill, M. O. 1979. Twinspan, a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. MP, Ithaka, NY.
- Hill, M. O., and H. G. Gauch. 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetatio* 42:47-58.
- Hoffman, M. T., B. Cousins, T. Meyer, A. Petersen, and H. Hendricks. 1999. Historical and contemporary land use and the desertification of the Karoo. Pages 257-273 in W. R. J. Dean and S. J. Milton, editors. *The Karoo*. Cambridge Univ Press.
- Hoffman, M. T., and R. M. Cowling. 1990. Vegetation change in the semi-arid eastern Karoo over the last 200 years: an expanding Karoo - fact or fiction? *South African Journal of Science* 86:286-294.
- Hoffman, T., and A. Ashwell. 2001. *Nature divided - Land degradation in South Africa*. University of Cape Town Press, Cape Town.
- Jaarsveld, E. J. v., and G. Williamson. 1994. *Tylecodon longipes* (Crassulaceae), a new species from the south-central Richtersveld (North-western Cape Province). *Aloe* 31:56-58.
- Jaarsveld, E. v. 1980. 'n Voorlopige Verslag oor die Plantegroei van die Richtersveld met Spesifieke Verwysing na die Bome en Struik van die Gebied. *Trees in South Africa* 32(3):58-84.
- Jaarsveld, E. v. 1981. *Aloe meyeri*: 'n Nuwe aalwyn van die Richtersveld (N.W.Kaap). *Veld & Flora*:72-73.
- Jaarsveld, E. v. 1989. The Richtersveld. *Excelsa* 14:55-56.
- Jaarsveld, E. v., and O. A. Leistner. 1992. The distribution of *Tylecodon* and *Cotyledon* (Crassulaceae) in South Africa and Namibia. *yyy*:1-6.
- Jacobs, A. 1996. Vegetationskundliche und ökophysiologische Untersuchungen an einem Landschaftsausschnitt der Nama-Kaoo-Region (Namibia). Unveröff. Diplomarbeit, Universität Köln.
- Jähnig, U. 1993. Charakterisierung arider Böden in der Namib unter besonderer Berücksichtigung der Vegetation (Nationalpark Richtersveld - Südafrika - und andere Standorte. Unveröff. Diplomarbeit. Universität Hamburg.
- Jongman, R. H. G., C. J. F. Ter Braak, and O. F. R. Tongeren van. 1995. *Data analysis in community and landscape ecology*. Cambridge University Press, Cambridge.
- Jürgens, N. 1986. Untersuchungen zur Ökologie sukkulenter Pflanzen des südlichen Afrika, Hamburg.
- Jürgens, N. 1990. A life form concept including anatomical characters, adapted for

- the description of succulent plants. Mitt. Inst. Allg. Bot. Hamburg 23a: 321-341.
- Jürgens, N. 1991. A new approach to the Namib Region. *Vegetatio* 97:21-38.
- Jürgens, N. 1997. Floristic biodiversity and history of African arid regions. *Biodiversity and Conservation* 6:495-514.
- Jürgens, N. 1998. Aspects of botanical biodiversity in southern African arid regions. An outline of concepts and results. Pages 53-70 in W. Barthlott and M. Winiger, editors. *Biodiversity. A Challenge for Development Research and Policy*. Springer-Verlag, Berlin, Heidelberg
- Jürgens, N., and A. Burke. 2000. The arid scenario: inselbergs in the Namib desert are rich oases in a poor matrix (Namibia & South Africa). Pages 237-258 in S. Porembski and W. Barthlott, editors. *Vegetation of Inselbergs*. Springer-Verlag, Berlin.
- Jürgens, N., A. Burke, M. K. Seely, and K. M. Jacobson. 1997. Desert. Pages 189-214 in R. M. Cowling and D. M. Richardson, editors. *Vegetation in Southern Africa*. Cambridge Univ.Press, Cambridge, UK.
- Jürgens, N., I. H. Gotzmann, and R. M. Cowling. 1999. Remarkable medium-term dynamics of leaf succulent Mesembryanthemaceae shrubs in the winter-rainfall desert of north-western Namaqualand, South Africa. *Plant Ecology* 142:87-96.
- Kadmon, R., and A. Danin. 1999. Distribution of plant species in Israel in relation to spatial variation in rainfall. *Journal of Vegetation Science* 10:421-432.
- Klak, C., and H. P. Linder. 1998. Systematics of *Psilocalon* N.E.Br. and *Caulipsilon* Klak gen. nov. (Mesembryanthemoideae, Aizoaceae). *Bot. Jahrb. Syst.* 120:301-375.
- Klein, R. G. 1988. The archaeological significance of animal bones from Acheulean sites in southern Africa. *The African Archaeological Review* 6:3-25.
- Knapp, R. 1968. Höhere Vegetationseinheiten von Äthiopien, Somalia, Natal, Transvaal, Kapland und einigen Nachbargebieten. II. Vegetations-Einheiten von Natal, Transvaal, Kapland und Nachbargebieten. *Geobot.Mitt.(Gieben)* 56:1-36.
- Knapp, R. 1973. *Die Vegetation von Afrika*. Fischer-Verlag, Stuttgart.
- Koch, C. 1962. The Tenebrionidae of Southern Africa XXXI. Comprehensive notes on the Tenebrionid fauna of the Namib desert. *Scient. Pap. Namib Desert Res. Stn.* 5:61-106.
- Koch, W. 1926. Die Vegetationseinheiten der Linthebene unter Berücksichtigung der Verhältnisse in der Nordostschweiz. *Jahrb. St. Gallische Naturwiss. Ges.* 61:1-144.
- Kutiel, P., and H. Lavee. 1999. Effect of slope aspect on soil and vegetation properties along an aridity transect. *Israel J.Bot.* 47:169-178.

- Larcher, W., U. Heber, and K. A. Santarius. 1973. Limiting temperatures for life functions. Pages 195-231 in H. Precht, J. Christophersen, H. Hensel, and W. Larcher, editors. *Temperature and life*. Springer-Verlag, Berlin.
- Leach, L. S. 1984. A new *Euphorbia* from the Richtersveld. *J.S.Afr.Bot.* 50(4):563-568.
- Lebrun, J. 1947. La végétation de la plaine alluviale au sud du lac Édouard. *Exploration des Parcs National Albert. Parcs National Congo Belge*, Brussels.
- Legendre, P., and E. D. Gallagher. 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia* 129:271-280.
- Legendre, P., and L. Legendre. 1998. *Numerical ecology*. Elsevier, Oxford.
- Leggett, K., J. Fennessy, and S. Schneider. 2003. Seasonal vegetation changes in the Hoanib River catchment, north-western Namibia: a study of a non-equilibrium system. *Journal of Arid Environments* 53:99-113.
- Leistner, O. A., and M. J. A. Werger. 1973. Southern Kalahari phytosociology. *Vegetatio* 28(5-6):353-399.
- Léonard, J. 2001. Flore et végétation du Jebel Uweinat (Désert de Libye, Egypte, Sudan). Sixième (et dernière) partie. *Etude de la végétation. Analyse phytosociologique des groupements végétaux*. Jardin Botanique National de Belgique, Meise.
- Linder, H. P., J. H. Vlok, D. J. McDonald, E. G. H. Oliver, C. Boucher, B.-E. v. Wyk, and A. Schutte. 1993. The high altitude flora and vegetation of the Cape Floristic Region, South Africa. *Opera Botanica* 121:247-261.
- Lloyd, J. W. 1989. Discriminant analysis and ordination of vegetation and soils on the Vaalputs radioactive waste disposal site, Bushmanland, South Africa. *South African Journal of Botany* 55(1):127-136.
- Lloyd, J. W. 1989. Phytosociology of the Vaalputs radioactive waste disposal site, Bushmanland, South Africa. *S.-Afr.Tydskr.Plantk.* 55(3):372-382.
- Loxton, R. F. 1962. The soils of the Republic of South Africa: A preliminary reclassification. *South African Journal of Science*:45-53.
- Maarel, E. v. d. 1979. Transformation of cover-abundance values in phytosociology and its effects on community similarity. *Vegetatio* 39, 2:97-114.
- Manning, J. C. 1990. A new species of *Trachyandra* section *Liriothamnus* (Asphodelaceae) from the Richtersveld. *South African Journal of Botany* 56:1-5.
- Marloth, R. 1887. Das südöstliche Kalahari-Gebiet. Ein Beitrag zur Pflanzengeographie Südafrikas. *Botanische Jahrbücher* 8:247-260.
- Marloth, R. 1908. *Das Kapland*. Fischer-Verlag, Jena.
- McCune, B. 1994. Improving community analysis with the Beals smoothing function. *Ecoscience* 1:82-86.
- McCune, B., and M. J. Mefford. 1999. *PC-ORD. Multivariate analysis of ecological data, Version 4*. MjM Software Designe, Oregon, USA.

- Merwe Van der, C. R. 1962. Soil groups and subgroups of South Africa. *Science Bulletin* 356.
- Merxmüller, H. 1972. *Prodromus einer Flora von Südwestafrika*. J. Cramer, Lehre.
- Midgley, G. F., and F. Heyden van der. 1999. Form and function in perennial plants. Pages 99-106 in W. Richard, J. Dean, and S. J. Milton, editors. *The Karoo. Ecological patterns and processes*. Cambridge University Press, Cambridge.
- Midgley, J. 1997. The decline of *Aloe pillansii* at Cornell's Kop in the Richtersveld. *Aloe* 1&2:1.
- Miller, D., and L. Webley. 1994. The metallurgical analysis of artefacts from Jakkalsberg, Richtersveld, northern Cape. *Southern African Field Archaeology* 3:82-93.
- Milton, S. J. 1991. Plant spinescence in arid southern Africa: does moisture mediate selection by mammals? *Oecologia* 87:279-287.
- Milton, S. J., R. I. Yeaton, W. R. J. Dean, and J. H. J. Vlok. 1997. Succulent Karoo. Pages 131-166 in R. M. Cowling, D. M. Richardson, and S. M. Pierce, editors. *Vegetation of Southern Africa*. Cambridge University Press.
- Milton, S. J., H. G. Zimmermann, and J. H. Hoffmann. 1999. Alien plant invaders of the Karoo: attributes, impacts and control. Pages 274-288 in W. R. J. Dean and S. J. Milton, editors. *The Karoo*. Cambridge Univ Press.
- Monod, T. 1957. *Les grands divisions chorologique de l'Afrique*. C.S.A./C.C.T.A., London.
- Mueller-Dombois, D., and H. Ellenberg. 1974. *Aims and methods of vegetation ecology*. Wiley & Sons, New York.
- Munsell 1994. *Munsell Soil Color Charts*. Macbeth Division of Kollmorgen Instruments Corporation, 405 Little Britain Road, New Windsor, NY 12553.
- Mussnug, U. 1995. An ethno-archaeological study of pastoralism along the Orange River at the Richtersveld. Pages 165-208 in A. B. Smith, editor. *Einiqualand. Studies of the Orange River frontier*. UCT Cape Town.
- NBI. 2003. *National Vegetation Map of South Africa Project (VEGMAP)*, research programme. [www.nbi.ac.za](http://www.nbi.ac.za).
- Oguz, I. 1999. *Vegetationsökologische Transektanalyse der Sandökosysteme im westlichen Richtersveld (Republik Südafrika)*. Unveröff. Examensarbeit, Universität Köln.
- Orshan, G. 1953. Note on the application of Raunkiaer's system of life forms in arid regions. *Palest. J. Bot. Jerusalem* 6:120-122.
- Orshan, G. 1964. Seasonal dimorphism of desert and Mediterranean chamaephytes and its significance in their water relations. Pages 206-222 in A. J. Ratter and F. H. Whitehead, editors. *Water in relation to plants*. Blackwell, Oxford.

- Orshan, G., and G. Sand. 1962. Seasonal body reduction of certain half shrubs. *Bull. Res. Counc. Isr.* 11:35-42.
- Osterloh, T. 2000. Vegetationsökologische Untersuchungen der Pioniervegetation an Kraalplätzen im Richtersveld (Republik Südafrika). Unveröff. Diplomarbeit, Universität zu Köln.
- Palgrave, K. C. 1993. *Trees of Southern Africa*, 2 edition. Struik, Cape Town.
- Palmer, A. R. 1989. The vegetation of the Karoo Nature Reserve, Cape Province. I Aphytosociological reconnaissance. *S. Afr. J. Bot.* 55:215-230.
- Palmer, A. R., and A. F. v. Rooyen. 1998. Detecting vegetation change in the southern Kalahari using Landsat TM data. *Journal of Arid Environments* 39:143-153.
- Pavon, N. P., H. Hernandez-Trejo, and V. Rico-Gray. 2000. Distribution of plant life forms along an altitudinal gradient in the semi-arid valley of Zapotitlan, Mexico. *Journal of Vegetation Science* 11:39-42.
- Penn, N. 1995. The Orange River Frontier Zone, C.1700-1805. Pages 21-109 in A. B. Smith, editor. *Einiqualand - Studies of the Orange River Frontier*. UCT Cape Town.
- Pettit, N. E., R. H. Froend, and P. G. Ladd. 1995. Grazing in remnant woodland vegetation: changes in species composition and life form groups. *Journal of Vegetation Science* 6:121-130.
- Pierce, S. M., and M. Gerbaulet. 1997. *Brownanthus Schwantes* (Mesembryanthemoideae, Aizoaceae): two new species and an new combination from the Richtersveld and south-western Namibia. *Aloe* 34:42-44.
- Poe Evans, I. B. 1922. The main botanical regions of South Africa. *Memoirs of the Botanical Survey of South Africa* 4:49-53.
- Pringle, J. A., C. Bond, and J. Clark. 1982. *The conservationists and the killers. The story of game protection and the Wilde Life Society of southern Africa.* Bulpin and Books of Africa, Cape Town: T. V.
- Quézel, P. 1965. *La Végétation du Sahara. Du Tchad à la Mauritanie.* Gustav Fischer-Verlag, Stuttgart.
- Raunkiaer, C. 1907. *Planterigetets Livsformer og deres Betydning for Geografien,* Kopenhagen.
- Reck, K. W. 1996. *Tracks and Trails of the Richtersveld.* K. W. Reck.
- Rehman, A. 1880. Geo-botaniczne stosunki potudniowwój Afryki. *Pamiętnik Akademii Umiejetnosci, Wydział Matematyczno-Przyrodniczy* 5:28-96.
- Rhoades, J. D. 1996. Salinity: Electrical conductivity and total dissolved solids. Pages 417-435 in D. L. Sparks, editor. *Methods of soil analysis, Part 3,* Madison.
- Roberts, M. R., and L. J. Wuest. 1999. Plant communities of New Brunswick in relation to environmental variation. *Journal of Vegetation Science* 10:321-334.

- Robinson, E. R. 1977. A plant ecological study of the Namib Desert. Unpublished M.Sc. Thesis. University of Natal, Pietermaritzburg.
- Rooyen, M. W. v., G. K. Theron, and N. Grobbelaar. 1990. Life form and dispersal spectra of the flora of Namaqualand, South Africa. *Journal of Arid Environments* 19:133-145.
- Ross, B. A., J. R. Tester, and W. J. Breckenridge. 1968. Ecology of Mima-type mounds in north-western Minnesota. *Ecology* 49:172-177.
- Roux, A., le, and C. Boucher. 1993. Flora of Namaqualand. Botanical Society of S.A. and NBI, Claremont.
- Roux, A. I. 1984. 'N fitososiologiese studie van die Hester Malan-Natuurreservaat. Univ. Pretoria.
- Roux, A. I., and E. A. C. L. E. Schelpe. 1988. Namaqualand. South African wild flower guide 1, 2 edition. Bot.Soc.S.A., Kirstenbosch.
- Rundel, P. W., K. J. Esler, and R. M. Cowling. 1999. Ecological and phylogenetic patterns of carbon isotope discrimination in the winter-rainfall flora of the Richtersveld. *Plant Ecology* 142:133-148.
- Rutherford, M. C. 1997. Categorization of biomes. Pages 91-98 in R. M. Cowling, D. M. Richardson, and S. M. Pierce, editors. *Vegetation of southern Africa*. Cambridge Univ. Press.
- Rutherford, M. C., and R. H. Westfall. 1986. Biomes of southern Africa - an objective categorization. *Mem. Bot. Surv. S. Afr.* 54:1-98.
- SANP. 1996. Richtersveld Management Plan. SANP.
- SANP. 1997. Richtersveld National Park - A World Heritage Site. Proposal SANP.
- Schmiedel, U. 2002. The quartz fields of Southern Africa. Doktorarbeit, Universität Hamburg.
- Schollenberger, J. 1993. The genus *Tylecodon* in the Richtersveld. *Aloe* 30,3/4:99-100.
- Schulte, A. 1994. Untersuchungen zur Vegetation der Sukkulente-Karoo (Südafrika) entlang eines grossräumigen Klimagradienten. Unveröff. Diplomarbeit, Universität Hamburg.
- Schulte, A. 2002. Weideökologie des Kaokolandes - Struktur und Dynamik einer Mopane-Savanne unter pastoralnomadischer Nutzung. Doktorarbeit, Universität Köln.
- Schüttler, G. 2002. Floristische und vegetationsökologische Analyse eines Höhengradienten im südlichen Richtersveld, Republik Südafrika. Unveröff. Diplomarbeit, Universität Köln.
- Scott, L. 1987. Pollen analysis of hyena coprolites and sediments from Equus Cave, Taung, Southern Kalahari (S. Africa). *Quaternary Research* 28:144-156.
- Scott, L. 1993. Palynological evidence for late Quaternary warming episodes in southern Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology*



- 101:229-235.
- Scott, L. 1994. Palynology of late Pleistocene hyrax middens, south-western Cape Province, South Africa: a preliminary report. *Historical Biology* 9:71-81.
- Scott, L. 1996. Palynology of hyrax middens: 2000 years of palaeoenvironmental history in Namibia. *Quaternary International* 33:73-79.
- Scott, L., H. M. Anderson, and J. M. Anderson. 1997. Vegetation history. Pages 62-90 in R. M. Cowling, D. M. Richardson, and S. M. Pierce, editors. *Vegetation of Southern Africa*. Cambridge Univ.Press.
- Scott, L., M. Steenkamp, and P. B. Beaumont. 1995. Palaeoenvironmental conditions in South Africa at the Pleistocene-Holocene transition. *Quat. Sci. Rev.* 14: 937-947.
- Smith, A. B. 1999. Hunters and herders in the Karoo landscape. Pages 243-256 in W. R. J. Dean and S. J. Milton, editors. *The karoo*. Cambridge Univ Press.
- Smith, A. B., D. Halkett, T. Hart, and B. Mütti. 2001. Spatial patterning, cultural identity and site integrity on open sites: Evidence from Bloeddrift 23, a pre-colonial herder camp in the Richtersveld, Northern Cape Province, South Africa. *South African Archaeological Bulletin* 56 (173 & 174):23-33.
- Solomon, M. 1997. Proposed research framework for Namaqualand. Alexkor, South-africa, (unpubl. script).
- Stöcker, B. 1999. Vegetationsökologische Untersuchungen zweier Landschaftsausschnitte in den Dünenfeldern des nördlichen Sandveldes (Republik Südafrika). Unveröff. Examensarbeit, Universität Köln.
- Strohbach, B. J., and T. P. Sheuyange. 2000. Vegetation survey of Namibia. Research Institute, Windhoek, Namibia (unpubl. script).
- Takhtajan, A. 1969. Flowering plants: Origin and dispersal. Oliver & Boyd, Edinburgh.
- Taylor, H. C. 1980. Phytogeography of Fynbos. *Bothalia* 13(1 &2):231-235.
- Ter Braak, C. J. F. 1986. Canonical Correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67:1167-1179.
- Ter Braak, C. J. F. 1994. Canonical community ordination. Part I: Basic theory and linear methods. *Ecoscience* 1:127-140.
- Ter Braak, C. J. F., and P. Smilauer. 1998. CANOCO reference manual and user's guide to Canoco for Windows. Software for canonical community ordination, version 4. Centre for Biometry, Wageningen.
- Troupin, G. 1966. Étude phytocénologique du Parc National de l'Akagera et du Rwanda oriental. Publications d'Institut National de Recherches Scientifiques Butare, Rwanda.
- Tüxen, R. 1974. Synchronologie einzelner Vegetationseinheiten in Europa. *Ebenda*: 265-292.

- Tüxen, R., and H. Ellenberg. 1937. Der systematische und ökologische Gruppenwert. Ein Beitrag zur Begriffsbildung und Methodik der Pflanzensoziologie. *Flor.-Soz. Arbeitsgem.* 3:171-184.
- van der Walt, J. J. A. 1977. *Pelargoniums of southern Africa*. Purnell & Sons, Cape Town.
- van der Walt, J. J. A., and P. J. Vorster. 1981. *Pelargoniums of southern Africa*. Vol. 2. Juta & Co., Johannesburg.
- van der Walt, J. J. A., and P. J. Vorster. 1988. *Pelargoniums of southern Africa*. Vol. 3. National Botanic Gardens, Kirstenbosch.
- van Zyl, L. 2000. A systematic revision of *Zygophyllum* (Zygophyllaceae) in the southern African region. Dissertation. University of Stellenbosch.
- Vetaas, O. R. 1993. Effect of spatial arrangement of environmental variables on ordination results from a distributed humidity gradient in north-eastern Sudan. *Coenoses* 8:27-37.
- Villiers, J. d., and P. G. Söhnge. 1959. The geology of the Richtersveld. *Geol. Surv. S. Afr.* 48:1-266.
- Vincent, A. S. 1985. Plant foods in savanna environments: a preliminary report of tubers eaten by the Hadza of northern Tanzania. *World Archaeology* 17:131-148.
- Visser, D. J. L. 1989. The Geology of the Richtersveld. *Geol. Surv. S. Africa Mem.* 48.
- Walter, H., and H. Lieth. 1963. *Klimadiagramm Weltatlas*, Jena.
- Walter, H. E. 1953. Einige allgemeine Ergebnisse unserer Forschungsreise nach Südwestafrika 1952/53: Das Gesetz der relativen Standortskonstanz; das Wesen der Pflanzengemeinschaften.
- Wand, S. J. E., K. J. Esler, P. W. Rundel, and H. W. Sherwin. 1999. A preliminary study of the responsiveness to seasonal atmospheric and rainfall patterns of wash woodland species in the arid Richtersveld. *Plant Ecol.* 142:149-160.
- Warren, S. D. 2001. Synopsis: Influence of biological soil crusts on arid land hydrology and soil stability. Pages 349-360 in J. Belnap and O. L. Lange, editors. *Biological soil crusts: structure, function, and management*. Springer-Verlag, Berlin, Heidelberg, New York.
- Warren, S. D., and D. J. Eldridge. 2001. Biological soil crusts and livestock in arid ecosystems: are they compatible? Pages 401-415 in J. Belnap and O. L. Lange, editors. *Biological soil crusts: structure, function, and management*. Springer-Verlag, Berlin, Heidelberg, New York.
- Watson, A. 1988. Desert gypsum crusts as palaeoenvironmental indicators: A micro-petrographic study of crusts from southern Tunisia and the central Namib Desert. *Journal of Arid Environments* 15:19-42.

- Weber, H. E., J. Moravec, and J.-P. Theurillat. 2000. International code of phytosociological nomenclature. 3rd edition. *Journal of Vegetation Science* 11:739-768.
- Webley, L. 1997. Jakkalsberg A and B: The cultural material from two pastoralist sites in the Richtersveld, Northern Cape. *S.Afr. Field Archaeology* 6:3-19.
- Webley, L., F. M. Archer, and J. Brink. 1993. Die Toon: A Late Holocene site in the Richtersveld National Park, northern Cape. *Koedoe* 36/2:1-9.
- Weidner, M. 1997. Ökophysiologische Untersuchungen an Pflanzen des Richtervelds. Unveröff. Skript, Universität Köln.
- Werger, M. J. A. 1886. Karoo and southern Kalahari. Pages 283-359 in M. Evenari, I. Noy-Meir, and D. W. Goodall, editors. *Ecosystems of the world - Hot deserts and arid shrublands*. Elsevier, Amsterdam.
- Werger, M. J. A. 1973. An account of the plant communities of Tussen die Riviere Game Farm, Orange Free State. *Bothalia* 11:165-176.
- Werger, M. J. A. 1978a. Biogeographical division of southern Africa. Pages 147-170 in M. J. A. Werger, editor. *Biogeography and Ecology of southern Africa*. W. Junk, The Hague.
- Werger, M. J. A. 1978b. The Karoo-Namib Region. Pages 231-299 in M. J. A. Werger, editor. *Biogeography and Ecology in Southern Africa*. W. Junk, The Hague.
- Werger, M. J. A., and B. J. Coetsee. 1977. A phytosociological and phytogeographical study of Augrabies Falls National Park, Republic of South Africa. *Koedoe* 20:11-51.
- Werger, M. J. A., and B. J. Coetsee. 1978. The Sudano-Zambeian Region. Pages 301-462 in M. J. A. Werger, editor. *Biogeography and Ecology of southern Africa*. Junk, The Hague.
- Werger, M. J. A., and J. W. Morris. 1991. Climatic control of vegetation structure and leaf characteristics along an aridity gradient. *Annali di Botanica* 11:203-215.
- White, F. 1965. The savanna woodlands of the Zambeian and Sudanian Domains: an ecological and phytogeographical comparison. *Webbia* 19:651-681.
- White, F. 1971. The taxonomic and ecological basis of chorology. *Mitt.Bot.München* 10:91-112.
- White, F. 1976. The vegetation map of Africa - The history of a completed project. *Boissiera* 24:659-666.
- White, F. 1983. The vegetation of Africa. A descriptive memoir to accompany the Unesco/AETFAT/UNSO vegetation map of Africa. Unesco, Paris.
- Wiegand, K., F. Jeltsch, and D. Ward. 1999. Analysis of the population dynamics of *Acacia* trees in the Negev desert, Israel with a spatially-explicit computer simulation model. *Ecological Modelling* 117:203-224.

- Williamson, G. 1990. The Richtersveld, a treasure-trove of succulent plants. *Aloe* 27, 2:34-39.
- Williamson, G. 1992. A new species of *Tylecodon* (Crassulaceae) from Namibia and a new variety from the Richtersveld in South Africa. *Aloe* 29,3/4:60-63.
- Williamson, G. 1994. *Anacampseros scopata* (Portulacaceae), a new species from the north-western Cape. *Cactus and Succulent Journal* 66:20-23.
- Williamson, G. 1995. Richtersveld National Park. Umdaus Press.
- Williamson, G. 1995. Two new *Tylecodon* species (Crassulaceae) from the southern Namib Desert (Namibia) and the Richtersveld (Cape Province, RSA). *Cactus and Succulent Journal* 67:114-118.
- Williamson, G. 1998. Aspects of the ecology of the Richtersveld succulent flora. *Aloe* 35:55-57.
- Williamson, G. 1998. *Ornithogalum scabrocostatum* U. & D. Müller-Doblies, a recently described succulent species from the Richtersveld. *Aloe* 35:25-26.
- Williamson, G. 2000. Richtersveld - The enchanted wilderness. Umdaus Press, Hatfield.
- Worcester, B. K., and K. J. Dalsted. 1979. Application of remote sensing to detection of desertification processes. Pages 622-628 in J. R. Goodin and D. K. Northington, editors. Arid land plant resources. Proc. of the Int. Arid Lands Conference on Plant Resources, Int. center for Arid and Semi-Arid Land Studies, Texas Tech Univ., Lubbock, Texas.
- Wyk, B. v., and P. v. Wyk. 1997. Field guide to trees of southern Africa, 1 edition. Struik Publ., Cape Town.
- Yamaguchi, Y., A. B. Kahle, H. Tsu, T. Kawakami, and M. Piel. 1998. Overview of advanced spaceborn thermal emission and reflection radiometer (ASTER). *IEEE Transactions on Geoscience and Remote Sensing* 36:1062-1071.

## 7. Index

### *Figures*

- Fig. 1.1: Topographical map of the Richtersveld. The frame marks the study area, which follows a climatic gradient from coast to inland (after Williamson 2000, modified). **9**
- Fig. 1.2: Topographical map of the Richtersveld with features of the defined landscape units. **11**
- Fig. 1.3: Geological map of the northern Richtersveld (data from Villiers & Söhnge 1959, simplified after Williamson 2000). **15**
- Fig. 1.4: Climatic diagrams of eight meteorological stations located within the north-western Cape Region (Walter & Lieth 1965). **21**
- Fig. 1.5: The two major climate regimes, winter rainfall and summer rainfall on the western coast of southern Africa. **22**
- Fig. 1.6: Phytogeographic division of the Karoo-Namib Region after Jürgens (1991). **24**
- Fig. 1.7: Phytogeographical division of the Richtersveld according to Jürgens (1991). **25**
- Fig. 1.8: Dominance or co-dominance of four plant life form sets in relation to biomes. **26**
- Fig. 2.1: Distribution of the relevés (points) within the study area, northern Richtersveld (total 871 relevés). **34**
- Fig. 3.1: Distribution of the relevés within the five basic landscape units. **49**
- Fig. 3.2: The result of the hierarchical cluster analysis (Sørensen index, Flexible beta : -0.5) on the basis of 515 relevés and 403 species, is shown in the dendrogram (overview). **50**
- Fig. 3.3: Total species number [n] of the northern Richtersveld landscape units. **52**
- Fig. 3.4: Mean species number [n] and mean ground cover [%] from the coast to the interior along the main climate gradients precipitation and temperature. **52**
- Fig. 3.5: Life form spectrum [%] within the northern Richtersveld. **53**
- Fig. 3.6: Life form spectra of the northern Richtersveld landscape units [%]. **53**
- Fig. 3.7: The percentage of two important growth forms, leaf and stem succulents in the western part (Succulent Karoo) and the eastern part (Nama Karoo) of the northern Richtersveld. **54**
- Fig. 3.8: Life form spectra of the main landscape units and the extrazonal Fynbos element. **57**
- Fig. 3.9: Amount of microbiotic and physical crusts, phytogenic mounds (PGM) and drown axis [%] in the whole Koeroegabvlakte (silty plain), northern Richtersveld. **70**

- Fig. 3.10: The erosion parameter along a descending gradient from the footslope to the end of the silty plain, Koeroegabvlakte, northern Richtersveld. **70**
- Fig. 3.11: Biplot of the Canonical Correspondence Analysis (CCA) for the data set of all 230 classified relevés. **97**
- Fig. 3.12: Joint plot of the Principal Components Analysis (PCA) of all 230 classified relevés. **98**
- Fig. 3.13: Joint plot of the Detrended Correspondence Analysis (DCA) of all 230 classified relevés. **98**
- Fig. 3.14: Biplot of the CCA for the data set of all 251 relevés with soil properties only, axis 1 and 2. **99**
- Fig. 3.15: Biplot of the CCA for the data set of all 251 relevés with soil properties only, axis 2 and 3. **100**
- Fig. 3.16: Biplot of the CCA for the data set of all 251 relevés with soil properties and all other variables. **101**
- Fig. 3.17: Biplot of the CCA for the habitats on the coastal plains. **103**
- Fig. 3.18: Joint plot of the Principal Components Analysis (PCA) for the habitats on the coastal plains. **104**
- Fig. 3.19: Biplot of the CCA for the slope habitats of the Richtersveld mountain region, axis 1 and 2. **105**
- Fig. 3.20: Biplot of the Canonical Correspondence Analysis (CCA) for the slope habitats of the Richtersveld mountain region, axis 1 and 3. **106**
- Fig. 3.21: Biplot of the CCA for the slope habitats of the Succulent Karoo. **107**
- Fig. 3.22: Biplot of the Canonical Correspondence Analysis (CCA) for the slope habitats of the Nama Karoo. **108**
- Fig. 3.23: Biplot of the CCA for the habitats of the flood plains and drainage lines. **110**
- Fig. 3.24: Ordination (CCA) and side scatter plots of differential species with species abundance as a function of ordination axis scores; comparison within the order level. **112**
- Fig. 3.25: Ordination (CCA) and side scatter plots of differential species with species abundance as a function of ordination axis scores; comparison within the alliance level. **113**
- Fig. 3.26: Ordination (CCA) and side scatter plots of *Didelta spinosa* with abundance as a function of ordination axis scores; comparison within the alliance level. **114**
- Fig. 3.27: Ordination (CCA) and side scatter plots of two differential species with abundance as a function of ordination axis scores; comparison within the association level: north-south exposure (N/S), e.g. at Koeroegab. **115**
- Fig. 3.28: Ordination (CCA) and side scatter plots of two differential species with abundance as a function of ordination axis scores; comparison within the

association level: north-south exposure (N/S), e.g. at Pooitjiespramberge. **116**

- Fig. 3.29: Ordination (CCA) and side scatter plots of two differential species with abundance as a function of ordination axis scores; comparison within the association level: south facing slopes, *Brownanthus nucifer*, north facing slopes, *Euphorbia virosa*. **117**
- Fig. 3.30: Ordination (CCA) and side scatter plots of two climatic variables, precipitation in winter and maximum air temperature in summer. **118**
- Fig. 3.31: Ordination (CCA) and side scatter plots of two soil variables, pH-value and stone content. **119**
- Fig. 4.1: Enhanced satellite image of the northern Richtersveld showing areas of higher plant biomass density (black to dark grey colours). Part of the coastal plain and the escarpment ranges show the highest canopy cover. **127**
- Fig. 4.2: Map showing locations of phytosociological investigations in southern Africa. **131**
- Fig. 4.3: Comparison of life form spectra of different study areas along the south-western coast and in N-E Africa. **140**
- Fig. 4.4: Map of the northern Richtersveld showing the distribution of stock posts within the national park area as was noted during the field work. **146**

#### Tables

- Tab. 1.1: Time scale of the geological events in the Richtersveld. (after Williamson 2000, modified). **17**
- Tab. 3.1: Relevé information for the syntaxa of the northern Richtersveld. **58**
- Tab. 3.2: Floristic and plant structural information for the syntaxa of the northern Richtersveld. **58**
- Tab. 3.3: Physical soil properties for the syntaxa of the northern Richtersveld. **59**
- Tab. 3.4: Chemical soil properties for the syntaxa of the northern Richtersveld. **59**

#### Appendix

- A. P1: West facing slope of the Maerpoortvlakte with flowering *Aloe gariepina*, eastern Gariep. **5**
- A. P2: View over the coastal plain (Sandveld) from the Goariiep mountains to the Atlantic Ocean. The bright points are the Mima-like mounds (*heuweltjies*). **177**
- A. P3: The 'Zygophyllum clavatum - Euphorbia brachiata association' on the sandy coastline. **177**
- A. P4: The 'Zygophyllum morgsana - Hermannia trifurca association' on the sandy inner-coastal plain. **178**
- A. P5: The 'Cheiridopsis robusta - Ruschia leucosperma association' of the 'Brownanthus pseudoschlichtianus - Drosanthemum inornatum alliance' on silty sand

- habitats of the coastal plain, firm sand ridge. **178**
- A. P6: The valley of the Numees mountains with *Pachypodium namaquanum*, escarpment. **179**
- A. P7: The 'Crassula grisea - Ruschia elineata association' at the Helskloof, escarpment 500 - 900 m. **179**
- A. P8: The 'Galenia africana - Prenia pallens association' on the Vandersterrberg; escarpment > 900 m. **180**
- A. P9: Drainage system of the Koeroegabvlakte, view to the north. **180**
- A. P10: The 'Cheilanthes capensis - Zygophyllum leptopetalum association' on a south facing slope of the Koeroegab. **181**
- A. P11: The 'Aridaria noctiflora s. noctiflora - Trachyandra muricata association' of the 'Brownanthus pseudoschlichtianus - Drosanthemum inornatum alliance' on silty sand habitats of the inner-mountain basins, Domoroghvlakte. **181**
- A. P12: Orange River valley at Pooitjiespram. **182**
- A. P13: Ganakouriep catchment of the eastern Gariep. **182**
- A. P14: Kokkerboomkloof with the 'Prenia tetragona - Psilocaulon subnodosum association' on gravelly flood plains. **183**
- A. P15: The 'Ceraria namaquensis - Aloe dichotoma alliance' of the eastern Gariep. **183**
- A. P16: The 'Euphorbia virosa - Euphorbia gariepina association' in the vicinity of the Orange River valley. **184**
- A. P17: The 'Sisyndite spartea - Rogeria longiflora association' on gravelly drainage lines; lower end of the Koeroegabvlakte drainage system. **184**
- A. P18: The 'Stipagrostis obtusa community' on the sandy Springbokvlakte, eastern Gariep. **185**
- A. P19: Dry shrub-land near Karasburg, Namibia, under summer rainfall regime. The dry shrub-land occurs in a distance of c. 300 km to the coast, north-east of the study area. **185**
- A. P20: Overburden of a diamond mine. The 'Brownanthus pubescens association' on the terraces of the Orange River valley is highly endangered by this destructive mining process. **186**
- A. P21: Initial phase of gully erosion on the silty Domoroghvlakte. **186**
- A. 1 Abbreviations **187**
- A. 2: Contour plots of the climatic variables which were used for the multivariate analyses. Data from Cramer & Leemans 1999, re-grided and interpolated (see section 2.4.2). Abbreviations as in A. 1. **188**
- A. 3: Scatterplot matrix of the climatic variables which were used as site descriptors for the multivariate analyses. Data from Cramer & Leemans 1999, re-grided and interpolated (see section 2.4.2). Abbreviations as in A. 1; DIS\_X330 =



- 
- distance to the coast (km), DIS\_Y330 = transect length parallel to the coast (km). **190**
- A. 4: Statistics summary for the data set of all 230 classified relevés (section 3.2.1): Spearman's correlation matrix for the environmental variables, forward selection parameters of the non-correlated variables, CCA eigenvalues, and Monte Carlo test results of the 'species-environment correlations'. For abbreviations see A. 1. **192**
- A. 5: Statistics summary for the data set of 251 relevés with soil properties only (section 3.2.2): Spearman's correlation matrix for the environmental variables, forward selection parameters of the non-correlated variables, CCA eigenvalues, and Monte Carlo test results of the 'species-environment correlations'. For abbreviations see A. 1. **193**
- A. 6: Statistics summary for the data set of 251 relevés with all environmental variables (section 3.2.3): Spearman's correlation matrix for the environmental variables, forward selection parameters of the non-correlated variables, CCA eigenvalues, and Monte Carlo test results of the 'species-environment correlations'. For abbreviations see A. 1. **194**
- A. 7: Statistics summary for the data set of the coastal plain habitats (section 3.2.4): Spearman's correlation matrix for the environmental variables, forward selection parameters of the non-correlated variables, CCA eigenvalues, and Monte Carlo test results of the 'species-environment correlations'. For abbreviations see A. 1. **196**
- A. 8: Statistics summary for the data set of the slope habitats (section 3.2.6): Spearman's correlation matrix for the environmental variables, forward selection parameters of the non-correlated variables, CCA eigenvalues, and Monte Carlo test results of the 'species-environment correlations'. For abbreviations see A. 1. **197**
- A. 9: Statistics summary for the data set of the Succulent Karoo slope habitats (section 3.2.6): Spearman's correlation matrix for the environmental variables, forward selection parameters of the non-correlated variables, CCA eigenvalues, and Monte Carlo test results of the 'species-environment correlations'. For abbreviations see A. 1. **198**
- A. 10: Statistics summary for the data set of the Nama Karoo slope habitats (section 3.2.7): Spearman's correlation matrix for the environmental variables, forward selection parameters of the non-correlated variables, CCA eigenvalues, and Monte Carlo test results of the 'species-environment correlations'. For abbreviations see A. 1. **199**
- A. 11: Statistics summary for the data set of the flood plains and drainage lines (section 3.2.8): Spearman's correlation matrix for the environmental variables, forward selection parameters of the non-correlated variables, CCA

eigenvalues, and Monte Carlo test results of the 'species-environment correlations'. For abbreviations see A. 1. **200**

- A. 12: Species list of the northern Richtersveld flora. **201**
- A. 13: List of the sample plots with relief and soil properties. **209**
- A. 14: Phytosociological table (see A. 13 for site descriptions). **216**

*Seperate tables and maps*

- A. T1: The result of the hierarchical cluster analysis (Sørensen index, Flexible beta : -0.5) on the basis of 515 relevés and 403 species, is shown in the dendrogram (detailed). **219**
- A. T2: Differentiated table of the sandy habitats on the coastal plain (Sandveld). **222**
- A. T3: Differentiated table of the silty habitats on the inner-mountain basins and the coastal plain. **224**
- A. T4: Differentiated table of the mountain slope habitats within the Succulent Karoo. **226**
- A. T5: Differentiated table of the mountain slope habitats within the Nama Karoo. **229**
- A. T6: Differentiated table of the gravelly habitats on flood plains and drainage lines. **230**
- A. T7: Synoptic table of the hierarchical classification of the northern Richtersveld vegetation. **232**
- A. T8: Preliminary vegetation map of the northern Richtersveld. **236**

## 8. Appendix



Photo A. P2: View over the coastal plain (Sandveld) from the Goariëp mountain to the Atlantic Ocean. The bright points are the Mima-like mounds (heuweltjies).



Photo A. P3: The 'Zygophyllum clavatum - Euphorbia brachiata association' on the sandy coastline.



Photo A. P4. The '*Zygophyllum morgsana* - *Hermannia trifurca* association' on the sandy inner-coastal plain.



Photo A. P5: The '*Cheiridopsis robusta* - *Ruschia leucosperma* association' of the '*Brownanthus pseudoschlichtianus* - *Drosanthemum inornatum* alliance' on silty sand habitats of the coastal plain, firm sand ridge.



Photo A. P6: The valley of the Numees mountains with *Pachypodium namaquanum*, escarpment.



Photo A. P7: The '*Crassula grisea* - *Ruschia elineata* association' at the Helskloof, escarpment 500 - 900 m.



Photo A. P8: The '*Galenia africana* - *Prenia pallens* association' on the Vandersterrberg; escarpment > 900 m.



Photo A. P9: Drainage system of the Koeroegabvlakte, view to the north.



Photo A. P10: The '*Cheilanthes capensis* - *Zygophyllum leptopetalum* association' on a south facing slope of the Koeroegab.



Photo A. P11: The '*Aridaria noctiflora* s. *noctiflora* - *Trachyandra muricata* association' of the '*Brownanthus pseudoschlichtianus* - *Drosanthemum inornatum* alliance' on silty sand habitats of the inner-mountain basins, Domoroghvlakte.



*Photo A. P12: Orange River valley at Pooitjiespram.*



*Photo A. P13: Ganakouriep catchment of the eastern Gariep.*





*Photo A. P14: Kokkerboomkloof with the 'Prenia tetragona - Psilocaulon subnodosum association' on gravelly flood plains.*

*Photo A. P15: The 'Ceraria namaquensis - Aloe dichotoma alliance' of the eastern Gariep.*



*Photo A. P16: The 'Euphorbia virosa - Euphorbia gariepina association' in the vicinity of the Orange River valley.*

*Photo A. P17: The 'Sisyndite spartea - Rogeria longiflora association' on gravelly drainage lines; lower end of the Koeroegabvlakte drainage system.*





Photo A. P18: The '*Stipagrostis obtusa* community' on the sandy Springbokvlakte, eastern Gariep.



Photo A. P19: Dry shrub-land near Karasburg, Namibia, under summer rainfall regime. The dry shrub-land occurs in a distance of c. 300 km to the coast, north-east of the study area.

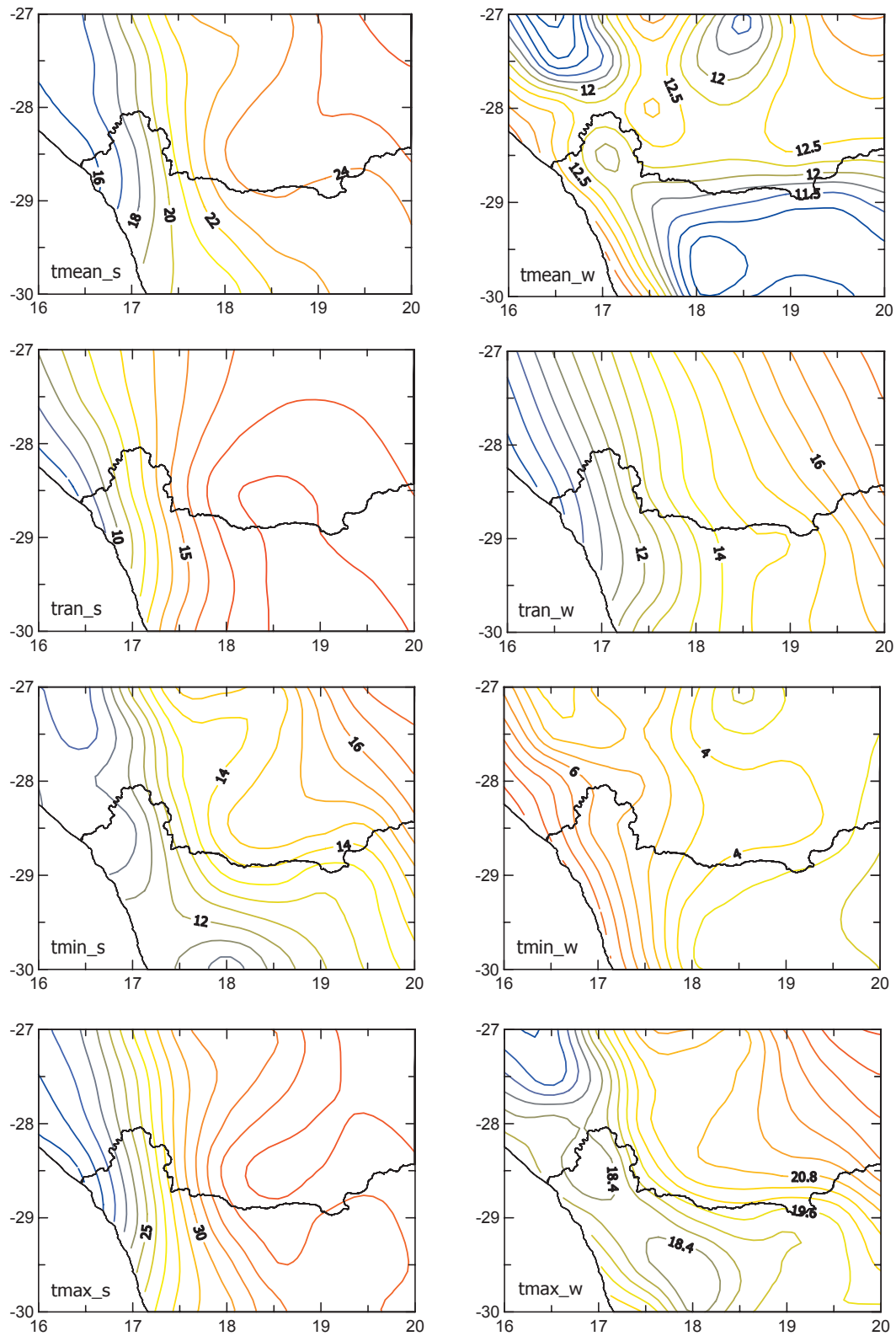


*Photo A. P20: Overburden of a diamond mine. The 'Brownanthus pubescens association' on the terraces of the Orange River valley is highly endangered by this destructive mining process.*

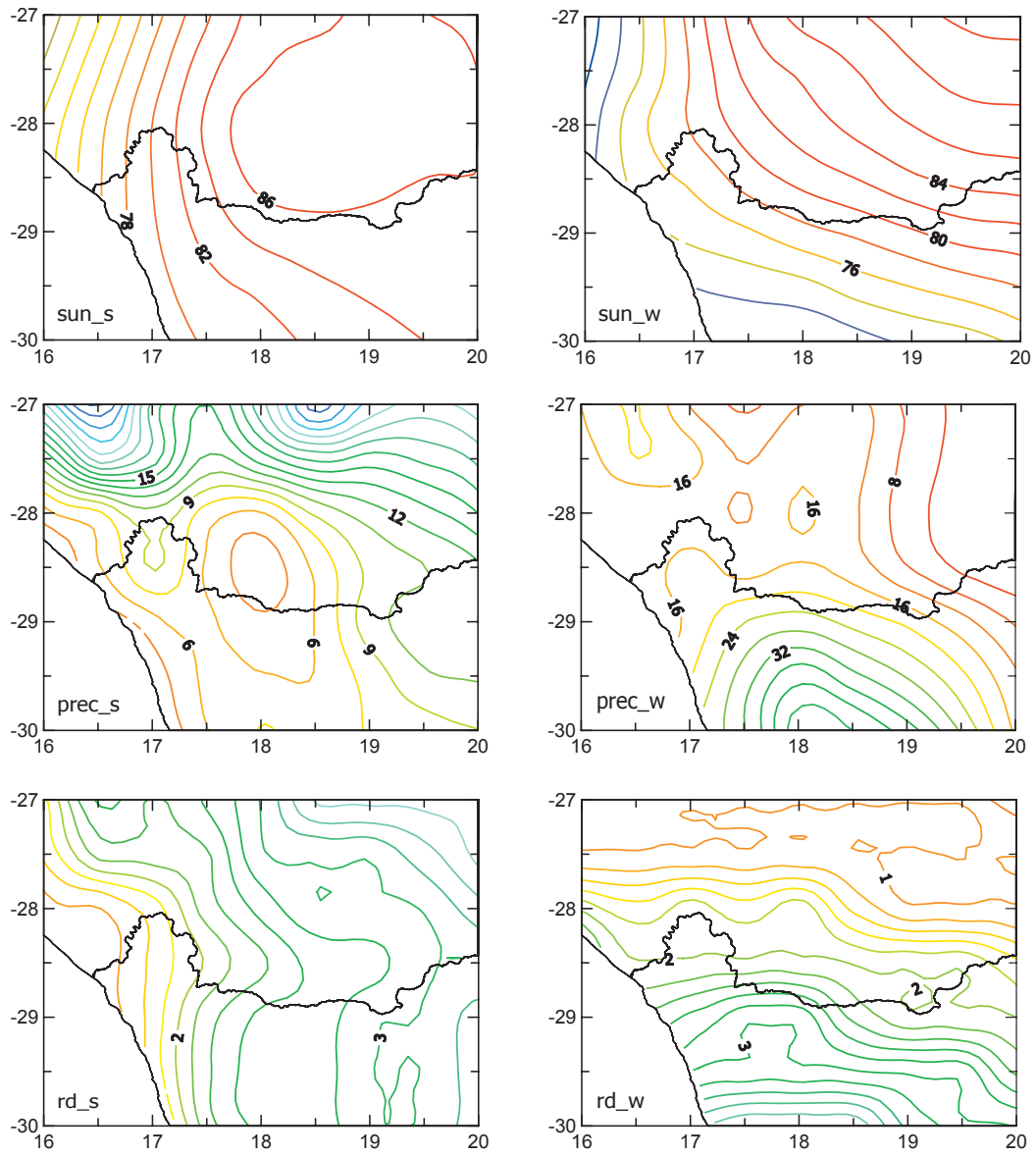
*Photo A. P21: Initial phase of gully erosion on the silty Domoroghvlakte.*

## A. 1: Abbreviations

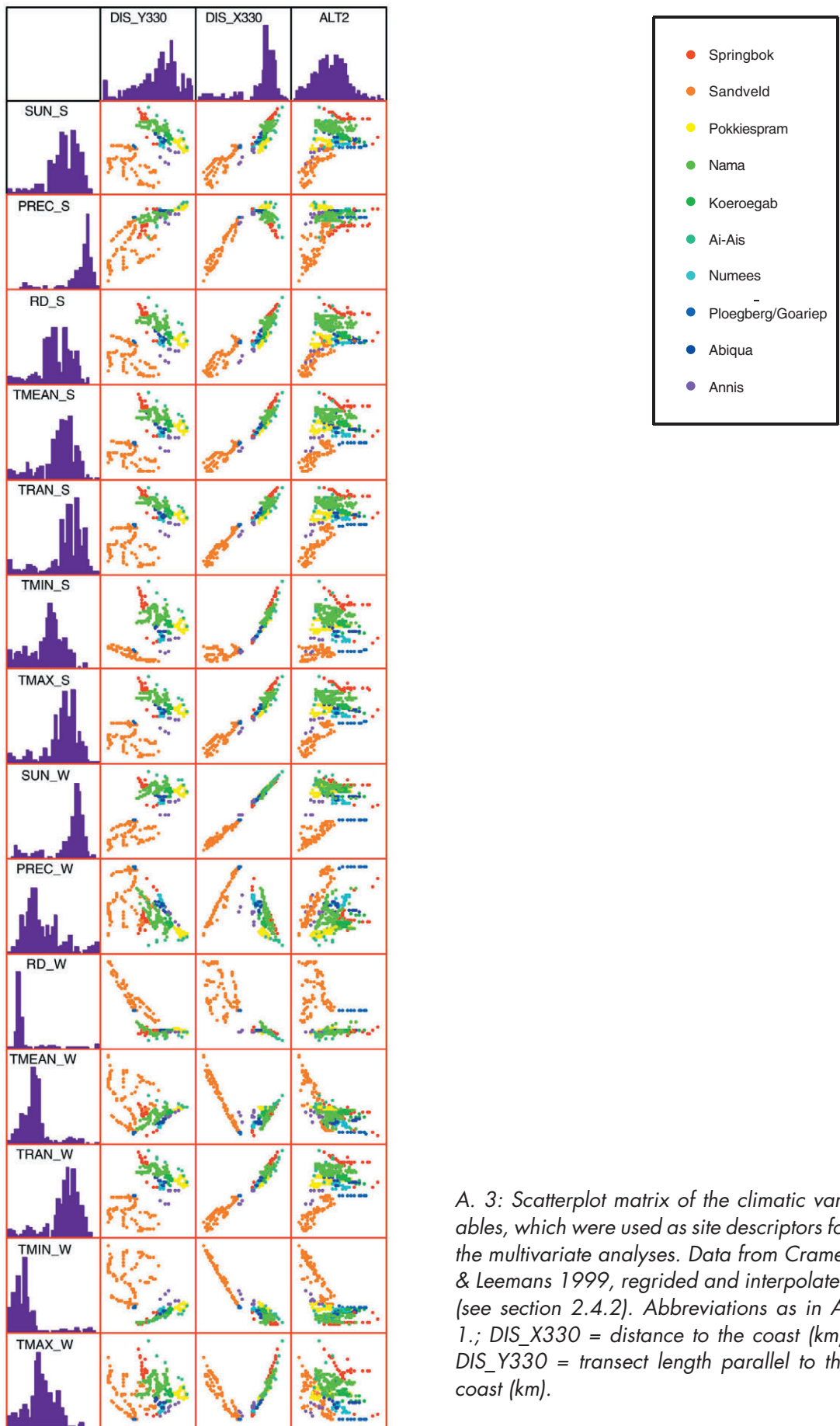
S	Sandveld (coastal plain)	GF	growth form	
Ps	silty plains	LF	life form	
Pg	gravely plains	T	therophytes	
Msk	mountain slopes within the Succulent Karoo	G	geophytes	
Mnk	mountain slopes within the Nama Karoo	H	hemicytrophytes	
		Ch	chamaephytes	
FNR	field number = sample number	NCh	nano-chamaephytes	0 - 5 cm
PNR	plot number = relevé number	MiCh	micro-chamaephytes	5 - 15 cm
		MCh	meso- to mega-chamaephytes	15 - 50 cm
		P	phanerophytes	
		NP	nano-phanerophytes	0.5 - 2 m
		MiP	micro-phanerophytes	2 - 5 m
		MP	mega-phanerophytes	> 5 m
		l	leaf	
s	stem	l ann	deciduous	
	s rept	l per	evergreen	
	s rut	l nan	dwarf-form	
	s frut	l red	reduced	
s su	stem succulent	l su	leaf succulent	
	s su lept	l su ann	deciduous	
	s su pach	l su per	evergreen	
		l su nan	dwarf-form	
r su	root succulent	l su red	reduced	
th	thorny			
CT	Chorotype	O, ord.	order	
CFR	Cape Floristic Region	sub-ord.	sub-order	
SKR	Succulent Karoo Region	all.	alliance	
NND	Namaqualand-Namib Domain	ass.	association	
SND	Southern Namib District	sub-ass.	sub-association	
WGC	Western Gariep Circle (Centre)	var.	variant	
NSDN	Northern Namaqualand Sandveld District	V1_V6	code of the hierarchical classification	
NSDS	Southern Namaqualand Sandveld District	D	differential species	
RVMD	Richtersveld Mountain District	C	constancy within the whole data set	
SKD	Southern Karoo Domain	Ct	constancy within the table	
NKR	Nama Karoo Region	Cwg	constancy within the group	
EKD	Eastern Karoo Domain	Cog	constancy outside the group	
ND	Namaland Domain	Co	companions	
NSUD	Namaland Subdomain			
NBSUD	Namib Subdomain			
ND	Namib District	S. within the taxa	subgenus	
EGD	Eastern Gariep District	s.	sub-species	
SZR	Sudano-Zambesian Region	v.	variant	
SPEC	species richness [n]	DIST/10	distance to the coast [km] / 10	
COV/10	total ground cover [%] / 10	ALT/100	altitude [m] / 100	
H-INDEXX	Shannon diversity index	INCL/10	inclination [°] / 10	
EVENESS	Pielou's evenness index	EAST	eastness [E,_W]	
		NORTH	northness [N,_S]	
GEO	geological unit			
G00	Quarantary sediments			
G01	coarse grained porphyritic granite (Tatasberg Complex and Kuboos Pluton)			
G02	medium grained non-porphyritic granite (Tatasberg Complex and Kuboos Pluton)			
G03	ultrametamorphosed mafic lava (Violsdrif Suite)			
G04	light coloured schist (Orange River Group)			
G05	dark coloured schist (Orange River Group)			
G06	mafic lava (Orange River Group)			
G07	quartzite, conglomerate, meta-quartzite, magnetite rich bands (Orange River Group)			
G08	gray, gneissic granite (Violsdrif Suite)			
G09	ultrametamorphosed sediment (Violsdrif Suite)			
G10	sheared greywacke and arkose (Schist) (Gariep Complex)	LAT	latitude	
G11	quartzite and sandstone (Stinkfontein Formation)	LONG	longitude	
G12	Tillite with lenses of shale and dolomite (Gariep Complex)	EXP	exposition	
_w	winter	S_Us	soil texture sandy silt	
_s	summer	S_mSu	soil texture silty medium sand	
_y	year	S_fSu	soil texture silty fine sand	
tmin	annual average monthly minimum air temperature	S_mS	soil texture medium sand	
tmax	annual average monthly maximum air temperature	Grev1, GR1	grevel [2 - 6 cm, %]	
tmean	annual average monthly mean air temperature	Grev2, GR2	grevel [< 2 cm, %]	
tran	annual average monthly air temperature range	Stone, ST	stone content [%]	
sun	annual average monthly sunshine percent	Fin	fine substrate	
prec	annual average monthly precipitation total	FinP	fine substrate conglomerate	
rd	annual average monthly number of rainy days	Carb, Log_Carb	carbonate content, log-transformed [Gew.%]	
pH	pH-value	Col1	colour	
EC, Log_EC	electrical conductivity, log-transformed [µS]	Col2	colour	



A. 2: Contour plots of the climatic variables, which were used for the multivariate analyses. Data from Cramer & Leemans 1999, gridded and interpolated (see section 2.4.2). Abbreviations as in A. 1.

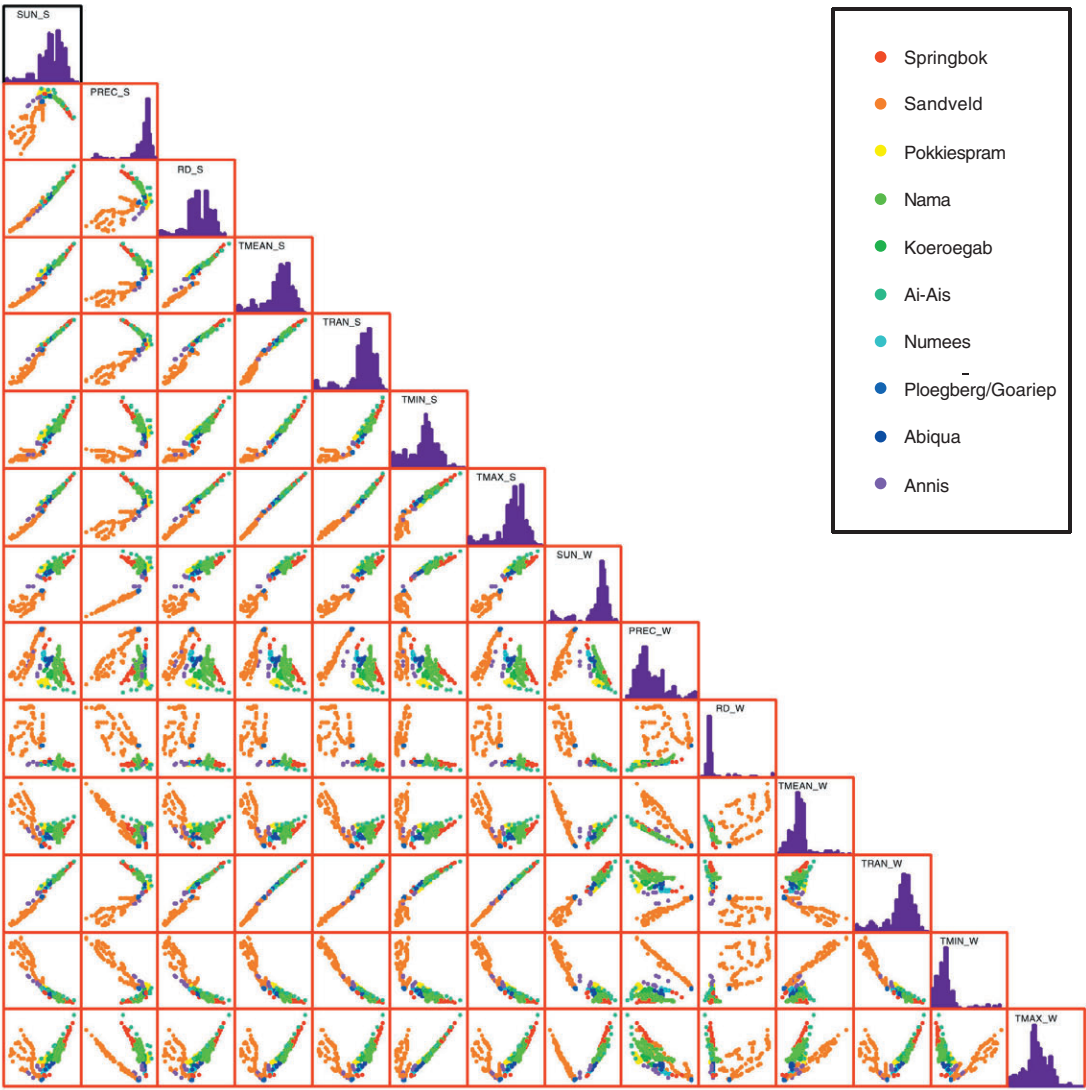


(A. 2, cont.)



A. 3: Scatterplot matrix of the climatic variables, which were used as site descriptors for the multivariate analyses. Data from Cramer & Leemans 1999, regrided and interpolated (see section 2.4.2). Abbreviations as in A. 1.; DIS\_X330 = distance to the coast (km), DIS\_Y330 = transect length parallel to the coast (km).





(A. 3, cont.)



### Spearman's correlation coefficient

pH	1.00														
LOG_EC	.44	1.00													
LOG_CARB	.51	.36	1.00												
COL1	.03	.05	.02	1.00											
COL2	.21	-.05	.17	.15	1.00										
Stone	-.06	-.02	-.09	.23	-.04	1.00									
Grav1	-.17	-.07	-.14	.31	-.20	.36	1.00								
Grav2	-.13	-.12	-.12	.29	-.28	.14	.58	1.00							
Fine	.12	.10	.12	-.31	.26	-.27	-.67	-.98	1.00						
FinP	.01	.19	.14	-.11	-.06	-.08	-.03	-.04	.05	1.00					
S_US	-.27	-.02	-.28	.19	-.24	-.04	.46	.42	-.41	.16	1.00				
S_MSU	-.03	-.20	-.01	.14	.10	.25	.13	.40	-.40	-.17	-.27	1.00			
S_FSU	.24	.19	.29	-.24	-.21	-.11	-.25	-.22	.23	.12	-.47	-.33	1.00		
S_MS	.04	-.02	-.01	-.05	.43	-.05	-.34	-.58	.56	-.16	-.31	-.22	-.38	1.00	

**Forward selection**

Marginal Effects

Variable	Var.N	Lambda 1
Grav2	8	0.46
S_mSu	12	0.36
S_Us	11	0.33
S_fSu	13	0.31
pH	1	0.21
LOG_EC	2	0.11

Conditional Effects

Variable	Var.N	Lambda A	P	F
Grav2	8	0.46	0.005	9.7
S_fSu	13	0.29	0.005	6.22
S_Us	11	0.25	0.005	5.66
S_mSu	12	0.24	0.005	5.24
pH	1	0.11	0.005	2.65
LOG_EC	2	0.09	0.005	1.87

**Eigenvalues**

Axes	1	2	3	4	inertia
Eigenvalues	0.545	0.357	0.259	0.132	11.847

Sum of all unconstrained eigenvalue 11.847  
Sum of all canonical eigenvalues 1.496

Monte Carlo test results: Species-Environment Correlations

Randomized data  
Real data Monte Carlo test, 99 runs

Axis	1	2	3
Spp-Envr Corr.	0.899	0.763	0.75
Mean	0.506	0.468	0.438
Minimum	0.421	0.413	0.369
Maximum	0.774	0.591	0.514
p	0.01	0.01	0.01

p = proportion of randomized runs with species-environment correlation greater than or equal to the observed species-environment correlation; i.e.,  
 $p = (1 + \text{no. permutations} \geq \text{observed}) / (1 + \text{no. permutations})$

A. 5: Statistics summary for the data set of 251 relevés with soil properties only (section 3.2.2): Spearman's correlation matrix for the environmental variables, Forward Selection parameters of the non-correlated variables, CCA eigenvalues, and Monte Carlo test results of the 'species-environment correlations'. For abbreviations see A. 1.

Forward selection

Marginal Effects

Variable	Var.N	Lambda 1
Grav2	33	0.46
tmean_w	15	0.42
S_mSu	37	0.36
S_Us	36	0.33
S_fSu	38	0.31
G08	45	0.29
pH	26	0.21
prec_w	13	0.13
EXP_180	4	0.11
LOG_EC	27	0.11
G06	44	0.1
Stone	31	0.1
G01	41	0.1
G02	42	0.08
G09	46	0.07
G04	43	0.07

Conditional Effects

Variable	Var.N	Lambda A	P	F
Grav2	33	0.46	0.01	9.7
tmean_w	15	0.31	0.01	6.79
S_Us	36	0.25	0.01	5.54
S_mSu	37	0.21	0.01	4.7
prec_w	13	0.16	0.01	3.57
pH	26	0.12	0.01	2.79
G02	42	0.11	0.02	2.46
S_fSu	38	0.1	0.01	2.38
G08	45	0.09	0.01	2.07
Stone	31	0.08	0.06	1.81
G01	41	0.07	0.19	1.75
G09	46	0.07	0.12	1.62
LOG_EC	27	0.07	0.01	1.6
EXP_180	4	0.06	0.08	1.31
G04	43	0.04	0.41	1.04
G06	44	0.03	0.63	0.59

Eigenvalues

Axes	1	2	3	4	inertia
Eigenvalues	0.578	0.458	0.286	0.155	11.847

Sum of all unconstrained eigenvalue 11.847  
Sum of all canonical eigenvalues 2.226

Monte Carlo test results: Species-Environment Correlations

Randomized data  
Real data Monte Carlo test, 99 runs

Axis	1	2	3
Spp-Envnt Corr.	0.922	0.849	0.771
Mean	0.578	0.547	0.519
Minimum	0.465	0.449	0.433
Maximum	0.92	0.711	0.59
p	0.01	0.01	0.01

p = proportion of randomized runs with species-environment correlation greater than or equal to the observed species-environment correlation; i.e.,  
 $p = (1 + \text{no. permutations} \geq \text{observed}) / (1 + \text{no. permutations})$

A. 6: Statistics summary for the data set of 251 relevés with all environmental variables (section 3.2.3): Spearman’s correlation matrix for the environmental variables, Forward Selection parameters of the non-correlated variables, CCA eigenvalues, and Monte Carlo test results of the ‘species-environment correlations’. For abbreviations see A. 1.



Spearman's correlation coefficient

SUN_S	1.00																		
PREC_S	.82	1.00																	
RD_S	1.00	.81	1.00																
TMEAN_S	.99	.78	.99	1.00															
TRAN_S	.99	.84	.99	.97	1.00														
TMIN_S	.52	.14	.53	.58	.49	1.00													
TMAX_S	1.00	.81	1.00	.99	.99	.53	1.00												
SUN_W	.84	.99	.83	.81	.87	.18	.84	1.00											
PREC_W	.46	.36	.46	.42	.47	-.15	.44	.39	1.00										
RD_W	-.49	-.75	-.48	-.45	-.52	.16	-.48	-.73	-.01	1.00									
TMEAN_W	-.84	-.91	-.83	-.80	-.86	-.07	-.83	-.92	-.70	.59	1.00								
TRAN_W	1.00	.82	1.00	.99	.99	.52	1.00	.84	.45	-.49	-.83	1.00							
TMIN_W	-.98	-.89	-.97	-.95	-.99	-.43	-.97	-.91	-.49	.55	.90	-.98	1.00						
TMAX_W	-.72	-.92	-.72	-.68	-.75	.13	-.72	-.90	-.63	.67	.96	-.72	.79	1.00					
S_FSU	.45	.45	.46	.41	.46	.48	.43	.46	-.03	-.10	-.31	.45	-.47	-.25	1.00				
S_MS	-.45	-.45	-.46	-.41	-.46	-.48	-.43	-.46	.03	.10	.31	-.45	.47	.25	-1.00	1.00			

Forward selection

Marginal Effects		
Variable	Var.N	Lambda 1
S_fSu	15	0.67
tran_w	12	0.54

Conditional Effects				
Variable	Var.N	Lambda A	P	F
S_fSu	15	0.67	0.005	5.18
tran_w	12	0.52	0.005	4.34

Eigenvalues

Axes	1	2	3	4	inertia
Eigenvalues	0.672	0.522	0.537	0.508	6.367

Sum of all unconstrained eigenvalues: 6.367  
Sum of all canonical eigenvalues: 1.194

Monte Carlo test results: Species-Environment Correlations

Randomized data  
Real data Monte Carlo test, 99 runs

Axis	1	2	3
Spp-Envt Corr.	0.974	0.926	0
Mean	0.692	0.667	0
Minimum	0.54	0.541	0
Maximum	0.834	0.809	0
p	0.01	0.01	1

p = proportion of randomized runs with species-environment correlation greater than or equal to the observed species-environment correlation; i.e.,  
p = (1 + no. permutations >= observed) / (1 + no. permutations)

A. 7: Statistics summary for the data set of the coastal plain habitats (section 3.2.4): Spearman's correlation matrix for the environmental variables, Forward Selection parameters of the non-correlated variables, CCA eigenvalues, and Monte Carlo test results of the 'species-environment correlations'. For abbreviations see A. 1.











Species	Authority	LF	GF	Synonym
<b>Pteridophyta</b>				
<b>Adiantaceae</b>				
Cheilanthes capensis	(Thunb.) Sw.	H	H	
Cheilanthes multifida	(Sw.) Sw.	H	H	
Cheilanthes robusta	(Kunze) R.M.Tryon	H	H	
<b>Aspleniaceae</b>				
Ceterach cordatum	(Thunb.) Desv.	G	G	
<b>Angiospermae</b>				
<b>Monocotyledonae</b>				
<b>Aloaceae</b>				
Aloe dichotoma	Masson	P	MIP S pach L su per	
Aloe gariepensis	Pillans	C	M-Ch L su per	
Aloe pearsonii	Schönland	P	NP L su per	
Aloe pillansii	L.Guthrie	P	MIP S pach L su per	
Aloe ramosissima	Pillans	P	MIP S pach L su per	
Gasteria pillansii v. ernesti-ruschi	Kensit (Dinter & Poelln.) Van Jaarsv.	C	Mi-Ch L su per	
Haworthia venosa s. tessellata	(Lam.) Haw. (Haw.) M.B.Bayer	C	Mi-Ch L su per	
<b>Asparagaceae</b>				
Asparagus aethiopicus	L.	P	NP	Protasparagus aethiopicus
Asparagus capensis	(L.) Oberm.	C	M-Ch	Protasparagus capensis
Asparagus exuvialis	Burch. fo. ecklonii (Baker) Fellingham & N.L.Mey.	G	G	Protasparagus exuvialis
Asparagus graniticus	(Oberm.) Fellingham & N.L.Mey.	C	M-Ch	Protasparagus graniticus
Asparagus juniperoides	Engl.	G	G	Myrsiphyllum juniperoides
Asparagus multituberosus	R.A.Dyer	G	G	Myrsiphyllum multituberosum
Asparagus retrofractus	L.	C	M-Ch	Protasparagus retrofractus
Asparagaceae 109530				
Myrsiphyllum asparagoides	(L.) Willd.	H	H	
<b>Asphodelaceae</b>				
Bulbine frutescens	(L.) Willd.	G	G L su	
Bulbine praemorsa	(Jacq.) Roem. & Schult.	G	G L su	
Trachyandra aridimontana	J.C.Manning	G	G L su	
Trachyandra bulbinifolia	(Dinter) Oberm.	G	G L su	
Trachyandra falcata	(L.f.) Kunth	G	G	
Trachyandra muricata	(L.f.) Kunth	G	G	
Trachyandra revoluta	(L.) Kunth	G	G L su	
<b>Colchicaceae</b>				
Androcymbium eucomoides	(Jacq.) Willd.	G	G	
Ornithoglossum parviflorum	B.Nord.	G	G	
Ornithoglossum viride	(L.f.) Aiton	G	G	
Ornithoglossum 112475		G	G	
<b>Cyperaceae</b>				
Carex 108661		T	T	
Carex 110543		T	T	
Cyperus marginatus	Thunb.	H	H	
<b>Eriospermaceae</b>				
Eriospermum 109527		G	G	
<b>Gramineae</b>				
Aristida adscensionis	L.	T	T	
Bromus pectinatus	Thunb.	H	H	
Cenchrus ciliaris	L.	H	H	
Chaetobromus dregeanus	Barker	H	H	
Chaetobromus involucreatus	(Schrad.) Nees	H	H	
Cladoraphis cyperoides	(Thunb.) S.M.Phillips	H	H	
Cladoraphis spinosa	(L.f.) S.M.Phillips	H	H	
Dregeochloa pumila	(Nees) Conert	H	H	
Ehrharta brevifolia v. cuspidata	Schrad. var. cuspidata Nees	T	T	
Ehrharta delicatula	(Nees) Stapf	T	T	
Ehrharta triandra	Nees ex Trin.	T	T	
Enneapogon desvauxii	P.Beauv.	T	T	
Enneapogon scaber	Lehm.	T	T	
Fingerhuthia africana	Lehm.	H	H	
Karoochloa schismoides	(Stapf ex Conert) Conert & Tüpe	H	H	
Leucophrys mesocoma	(Nees) Rendle	H	H	
Merxmüllera dura	Stapf) Conert	H	H	
Pennisetum species		H	H	
Pentastichis airoides s. airoides	(Nees) Stapf	H	H	
Schismus barbatus	(Loefl. ex L.) Thell.	T	T	
Stipagrostis anomala	De Winter	H	H	
Stipagrostis ciliata	(Desf.) De Winter	H	H	
Stipagrostis dinteri	(Hack.) De Winter	H	H	
Stipagrostis dregeana	Nees	H	H	
Stipagrostis geminifolia	Nees	H	H	
Stipagrostis lutescens	(Nees) De Winter	H	H	
Stipagrostis namaquensis	(Nees) De Winter	C	M-Ch	
Stipagrostis obtusa	(Delile) Nees	H	H	
Stipagrostis subcaulis	(Nees) De Winter	H	H	
Tribolium utriculosum	(Nees) Renvoize	H	H	
Gramineae 108982		T	T	
Gramineae 109552		T	T	
<b>Hyacinthaceae</b>				
Albuca maxima	Burm.f.	G	G L su	Albuca altissima
Albuca spiralis	L.f.	G	G L su	

A. 12: Species list of the northern Richtersveld flora.

Species	Authority	LF	GF	Synonym
Bowiea gariepensis	Van Jaarsv.	G	G L su ann	
Dipcadi crispum v. tortile	Baker	G	G L su	
Massonia depressa	Houtt.	G	G L su	
Ornithogalum decus-montium	G.Will.	G	G	
Ornithogalum suaveolens	Jacq.	G	G	
Ornithogalum xanthochlorum	Baker	G	G	
Veltheimia capensis	(L.) DC.	G	G	
<b>Iridaceae</b>				
Ferraria divaricata	Sweet	G	G	
Ferraria divaricata s. aurea	Sweet M.P.de Vos	G	G	
Ferraria schaeferi	Dinter	G	G	
Lapeirousia barklyi	Baker	G	G	
Moraea fugax s. filicaulis	(D.Delaroche) Jacq. (Baker) Goldblatt	G	G	
Moraea tortilis	Goldblatt	G	G	
<b>Dicotyledonae</b>				
<b>Acanthaceae</b>				
Acanthopsis disperma	Nees	T	T	
Acanthopsis spathularis	(E.Mey.) Schinz	H	H	
Blepharis furcata	(L.f.) Pers.	C	Mi-Ch	
Blepharis pruinosa	Engl.	C	Mi-Ch	
Justicia cuneata	Vahl	C	M-Ch	
Monechma cleomoides	(S.Moore) C.B.Clarke	C	M-Ch	Monechma arenicola
Monechma genistifolium	(Engl.) C.B.Clarke	C	M-Ch	
Monechma incanum	(Nees) C.B.Clarke	P	NP	
Monechma mollissimum	(Nees) P.G.Mey.	P	NP	Monechma molle
Monechma spartioides	(T.Anderson) C.B.Clarke	P	NP	
<b>Aizoaceae</b>				
<b>Aizooidae</b>				
Galenia africana	L.	C	M-Ch S frut L subsu ann	
Galenia collina	(Eckl. & Zeyh.) Walp.	C	M-Ch S frut L subsu ann	
Galenia crystallina	(Eckl. & Zeyh.) Fenzl	C	M-Ch S frut L subsu ann	
Galenia dregeana	Fenzl ex Sond.	C	M-Ch S frut L subsu ann	
Galenia fruticosa	(L.f.) Sond.	C	M-Ch S frut L subsu ann	
Galenia meziana	K.Müll.	H	H S rept frut	
Galenia namaensis	Schinz	C	M-Ch S frut L subsu ann	
Galenia squamulosa	(Eckl. & Zeyh.) Fenzl	C	M-Ch S frut L subsu ann	
Aizoaceae 109444				
<b>Mesembryanthemoideae</b>				
Aridaria brevicarpa	L.Bolus	C	M-Ch S frut L su ann	
Aridaria noctiflora s. noctiflora	(L.) Schwantes	H	M-Ch/H S frut L su ann r suc	
Aridaria serotina	L.Bolus	C	M-Ch S frut L su ann	
Aridaria 118036				
Brownanthus arenosus	(Schinz) Ihlenf. & Bittrich	C	M-Ch S lept L su ann	
Brownanthus ciliatus s. schenkii	(Aiton) Schwantes	C	M-Ch S lept L su ann	
Brownanthus nucifer	(Ihlenf. & Bittrich) S.M.Pierce & Gerbaulet	C	M-Ch S lept L su ann	
Brownanthus pseudoschlichtianus	S.M.Pierce & Gerbaulet	C	M-Ch S lept L su ann	
Brownanthus pubescens	(N.E.Br. ex C.A.Maass) Bullock	C	M-Ch S lept L su ann	
Hartmanthus pergamentaceus	(L.Bolus) S.A.Hammer	C	Mi-Ch L su per	
Mesembryanthemum garlusanum	Dinter FR	T	T S L su	
Mesembryanthemum guerichianum	Pax	T	T S rept L su	Mesembryanthemum gyrichanum
Mesembryanthemum hypertrophicum	Dinter	T	T S L su	
Mesembryanthemum pellitum	Friedrich	T	T S L su	
Mesembryanthemum squamulosum	(L.Bolus) L.Bolus	T	T S L su	Mesembryanthemum guerichanum
Mesemb 108697				
Mesemb 109534				
Opophytum aquosum	(L.Bolus) N.E.Br.	T	T S rept L su	Mesembryanthemum hypertrophicum
Phyllobolus deciduus	(L.Bolus) Gerbaulet	C	M-Ch S frut L su ann	Sphalmanthus deciduus
Phyllobolus decurvatus	(L.Bolus) Gerbaulet	C	M-Ch S frut L su ann per	Sphalmanthus decurvatus
Phyllobolus melanospermus	(Dinter & Schwantes) Gerbaulet	C	M-Ch S frut L su ann per	Sphalmanthus melanospermus
Phyllobolus ocellatus	(N.E.Br.) Gerbaulet	G	G S rept L su	Sphalmanthus scintillans
Phyllobolus species		C	M-Ch S frut L su ann per	Sphalmanthus sp. nov.
Phyllobolus species nov. 1		C	M-Ch S frut L su ann per	Sphalmanthus sp. nov.
Phyllobolus species nov. 2		C	M-Ch S frut L su ann per	Sphalmanthus sp. nov.
Phyllobolus 106540.2		C	M-Ch S frut L su	
Prenia pallens	(Aiton) N.E.Br.	T	Mi-Ch/T S rept L su ann per	
Prenia sladeniana	(L.Bolus) L.Bolus	T	Mi-Ch/T S rept L su ann per	
Prenia tetragona	(Thunb.) Gerbaulet	C	M-Ch S frut L su ann per	Sphalmanthus tetragonus
Psilocaulon dinteri	(Engl.) Schwantes	P	NP S lept L su ann per	
Psilocaulon dinteri inland	(Engl.) Schwantes	P	NP S lept L su ann per	
Psilocaulon foliosum	L.Bolus	P	NP S frut L su ann per	
Psilocaulon salicornioides	(Pax) Schwantes	C	M-Ch S lept L su ann	
Psilocaulon salicornioides creeping		C	M-Ch S rept lept L su ann	
Psilocaulon subnodosum	(A.Berger) N.E.Br.	P	NP S lept L su ann per	
<b>Ruschioideae</b>				
Amphibolia rupis-arcuatae	(Dinter) H.E.K.Hartmann	C	M-Ch S frut L su per	
Antimima compressa	(L.Bolus) H.E.K.Hartmann	C	M-Ch S frut L su per	
Antimima crassifolia	(L.Bolus) H.E.K.Hartmann	C	M-Ch S frut L su per	
Antimima perforata	(L.Bolus) H.E.K.Hartmann	C	M-Ch S frut L su per	
Antimima S. Clavipes kahn		C	M-Ch S frut L su per	
Antimima watermeyer	(L.Bolus) H.E.K.Hartmann	C	M-Ch S frut L su per	
Arenifera stylosa	(L.Bolus) H.E.K.Hartmann	C	M-Ch S frut L su per th	
Astridia alba	(L.Bolus) L.Bolus	C	M-Ch S frut L su per	Astridia longifolia
Astridia speciosa	L.Bolus	C	M-Ch S frut L su per	
Cephalophyllum ebracteatum	(Pax ex Schltr. & Diels) Dinter & Schwantes	C	Mi-Ch S rept L su per	
Cephalophyllum goodii	L.Bolus	C	Mi-Ch S rept L su per	
Cephalophyllum numeesense	H.E.K.Hartmann	C	Mi-Ch S rept L su per	
Cephalophyllum rigidum	L.Bolus	C	Mi-Ch S rept L su per	
Cheiridopsis alata	L.Bolus	C	Mi-Ch L su per	
Cheiridopsis denticulata	(Haw.) N.E.Br.	C	Mi-Ch L su per	
Cheiridopsis robusta	(Haw.) N.E.Br.	C	Mi-Ch L su per	
Cheiridopsis verrucosa	L.Bolus	C	Mi-Ch L su per	
Conicosia elongata	(Haw.) N.E.Br.	G	G	Herrea elongata
Conophytum bolusiae s. primavernum	Schwantes S.A.Hammer	C	N-Ch L su per	
Conophytum herreanthus s. herreanthus	S.A.Hammer	C	N-Ch L su per	
Conophytum herreanthus subsp. rex	S.A.Hammer	C	N-Ch L su per	

A. 12: Species list of the northern Richtersveld flora (cont.)

Species	Authority	LF	GF	Synonym
Conophytum jucundum	(N. E. Br.) N. E. Br.	C	N-Ch L su per	Conophytum gratum s. gratum
Conophytum meyeri	N.E.Br.	C	N-Ch L su per	
Delosperma crassum	L.Bolus	C	M-Ch S frut L su per	
Dracophilus dealbatus	(N.E.Br.) Walgate	C	Mi-Ch L su per	
Drosanthemum hispidum	(L.) Schwantes	C	M-Ch S frut L su per	
Drosanthemum inornatum	(L.Bolus) L.Bolus	C	M-Ch S frut L su per	
Drosanthemum luederitzii	(Engler) Schwantes	C	M-Ch S frut L su per	Drosanthemum paxianum
Drosanthemum muirii	L.Bolus	C	M-Ch S frut L su per	
Drosanthemum ramosissimum	(Schltr.) L.Bolus	C	M-Ch S frut L su	
Eberlanzia cyathiformis	(L.Bolus) H.E.K.Hartmann	C	M-Ch S frut L su per	
Eberlanzia sedoides big blue-green		C	M-Ch S frut L su ann per	
Eberlanzia ebracteata coast	(L.Bolus) H.E.K.Hartmann	C	M-Ch S frut L su per	
Eberlanzia ebracteata inland	(L.Bolus) H.E.K.Hartmann	C	M-Ch S frut L su per	
Eberlanzia schneideriana	(A.Berger) H.E.K. Hartmann	C	M-Ch S frut L su per	
Eberlanzia sedoides	(Dinter & A. Berger) Schwantes	C	M-Ch S frut L su per	
Fenestraria rhopalophylla	(Schltr. & Diels) N.E.Br.	C	N-Ch L su per	
Jordaniella clavifolia	(L.Bolus) H.E.K.Hartmann	C	Mi-Ch S rept L su per	Jordaniella cuprea kleinblättrig
Jordaniella cuprea	(L.Bolus) H.E.K.Hartmann	C	Mi-Ch S rept L su per	
Jordaniella spongiosa	(L. Bolus) H. E. K. Hartmann	C	M-Ch S rept L su per	Cephalophyllum spongiosum
Lampranthus 6 valves		C	M-Ch S frut L su per	
Lampranthus hoerleinianus	(Dinter) Friedrich	C	M-Ch S frut L su per	
Lampranthus otzenianus	(Dinter) Friedrich	C	M-Ch S frut L su per	
Lampranthus suavissimus	(L.Bolus) L.Bolus	C	M-Ch S frut L su per	
Leipoldtia alborosea	(L.Bolus) H.E.K.Hartmann & Stüber	C	Mi-Ch S rept L su per	
Leipoldtia Numees		C	Mi-Ch S rept L su per	
Leipoldtia schultzei	(Schltr. & Diels) Friedrich	C	Mi-Ch S rept L su per	
Leipoldtia weingangiana	(Dinter) Dinter & Schwantes	C	Mi-Ch S rept L su per	
Mitrophylum clivorum	(N.E.Br.) Schwantes	C	M-Ch S lept L su	
Ruschia abbreviata	L.Bolus	C	M-Ch S lept L su per	Ruschia subaphylla
Ruschia atrata	L.Bolus	C	M-Ch S frut L su ann per	Ruschia subg. Stricta atrata
Ruschia brevibracteata	L. Bolus	C	M-Ch S rept frut L su per	PC R. extensa
Ruschia brevifolia	L.Bolus	C	M-Ch S frut L su per	
Ruschia elineata	L.Bolus	C	M-Ch S frut L su per	Ruschia endständig
Ruschia inconspicua	L.Bolus	C	M-Ch S frut L su per	
Ruschia leucosperma	L.Bolus	C	M-Ch S frut L su ann per	Ruschia subg. Stricta leucosperma
Ruschia middlemostii	L.Bolus	C	M-Ch S frut L su per	Antimima middlemostii
Ruschia Sarmatosa ascending fruits		C	M-Ch S rept frut L su per	
Ruschia senaria	L.Bolus	C	M-Ch S frut L su per	
Ruschia spinosa	(L.) Dehn	C	M-Ch S frut L su per th	
Ruschia Tumidula black fruits		C	M-Ch S frut L su per	
Ruschia Tumidula black fruits creeping		C	M-Ch S rept frut L su per	
Ruschia vanheerdei	L.Bolus	C	M-Ch S frut L su per	
Ruschianthemum gigas	(Dinter) Friedrich	P	NP S frut L su per	
Ruschia 106356		C	M-Ch S frut L su per	
Ruschia 106357a		C	M-Ch S frut L su per	
Ruschia 109373		C	M-Ch S frut L su per	
Ruschia 109446		C	M-Ch S frut L su per	
Schwantesia acutipetala	L.Bolus	C	Mi-Ch L su per	
Schwantesia herrei	L.Bolus	C	Mi-Ch L su per	
Stoebertia arborea	Van Jaarsv.	C	M-Ch S frut L su per	
Stoebertia beetzii	(Dinter) Dinter & Schwantes	C	M-Ch S frut L su per	
Stoebertia carpii	Friedrich	C	M-Ch S frut L su per	
Stoebertia frutescens	(L. Bolus) Van Jaarsveld	P	MiP S frut L su per	
Stoebertia utilis	(L. Bolus) Van Jaarsveld	P	NP S frut L su per	
<b>Sesuvioideae</b>				
Sesuvium sesuvioides	(Fenzl) Verdc.	T	T S L su	
Trianthema triquetra	Willdenow ex Sprengel	T	T S rept L su	
<b>Tetragonioideae</b>				
Tetragonia arbuscula	Fenzl	C	M-Ch L subsu ann	
Tetragonia echinata	Aiton	T	T S rept L subsu	
Tetragonia fruticosa	L.	C	M-Ch L subsu ann	
Tetragonia reduplicata	Welw. ex Oliv.	C	M-Ch/NP S frut L su ann r suc	
Tetragonia spicata	L.f.	T	T L subsu ann	
<b>Amaranthaceae</b>				
Callicorema capitata	(Moq.) Hook.f.	P	NP	
Callicorema squarrosa	(Schinz) Schinz	C	M-Ch	
Hermbsstaedia glauca	(J.C.Wendl.) Rchb. ex Steud.	C	NP/M-Ch S rut	
Sericocoma heterochiton	Lopr.	C	M-Ch	
Gethyllis namaquensis	(Schönland) Oberm.	G	G	
<b>Anacardiaceae</b>				
Ozoroa concolor	(C.Presl ex Sond.) De Winter	P	MiP/NP L ann	
Ozoroa dispar	(C.Presl) R. & A.Fern.	P	MiP/NP L ann	
Rhus lancea	L.f.	P	MiP	Rhus viminalis
Rhus pendulina	Jacq.	P	MiP	
Rhus populifolia	E.Mey. ex Sond.	P	NP	
Rhus undulata	Jacq.	P	NP	
Rhus undulata x populifolia		P	NP	
Schinus molle	L.	P	NP	
<b>Apocynaceae</b>				
Carissa haematocarpa	(Eckl.) A.DC.	P	MiP L per	
Pachypodium namaquanum	(Wyley ex Harv.) Welw.	P	NP/MiP S pach L subsu ann	
<b>Asclepiadaceae</b>				
Asclepias cancellata	(Burm.f.) Bruyns	P	NP	
Curroria decidua	Planch. ex Hook.f. & Benth.	P	NP	Asclepias fruticosa
Gomphocarpus fruticosus	(L.) Aiton f.	P	NP	
Hoodia alstonii	(N.E.Br.) Plowes	P	NP S pach L red	
Hoodia gordonii	(Masson) Sweet ex Decne.	P	NP S pach L red	
Larryleachia dinteri	(A.Berger) Plowes	C	Mi-Ch S pach	
Microloma calycinum	E.Mey.	C	M-Ch	
Microloma incanum	Decne.	C	M-Ch	
Microloma sagittatum	(L.) R.Br.	C	M-Ch	
Notechidnopsis colummaris	(Nel) Lavranos & Bleck	C	Mi-Ch L red	
Orbea namaquensis	(N.E.Br.) L.C.Leach	C	N-Ch	
Quaqua acutiloba	(N.E.Br.) Bruyns	C	Mi-Ch L red	
Sarcostemma viminalis	(L.) R.Br.	C	M-Ch/NP S lept L red	

Species	Authority	LF	GF	Synonym
<i>Stapelia garipeensis</i>	Pillans	C	Mi-Ch L red	
<i>Tromotriche aperta</i>	Bruyns	C	Mi-Ch S L red	
<i>Tromotriche longipes</i>	(C.A.Lückh.) Bruyns	C	Mi-Ch S L red	
<i>Tromotriche umdausensis</i>	(Nel) Bruyns	C	Mi-Ch S L red	
<b>Boraginaceae</b>				
<i>Amsinckia menziesii</i>	(Lehm.) A.Nelson & J.F.Macbr.	T	T	
<i>Heliotropium tubulosum</i>	E.Mey. ex DC.	T	T	
<i>Trichodesma africanum</i>	(L.) Lehm.	T	T/Ch S	
<i>Wellstedtia dinteri</i>	Pilg.	C	M-Ch	
<b>Burseraceae</b>				
<i>Commiphora capensis</i>	(Sond.) Engl.	P	NP S pach L ann	
<i>Commiphora gracilifronsosa</i>	Dinter ex J.J.A.van der Walt	P	NP S pach L ann	
<b>Campanulaceae</b>				
<i>Cyphia longiflora</i>	Schltr.	H	H	
<i>Wahlenbergia annularis</i>	A.DC.	T	T	
<i>Wahlenbergia meyeri</i>	A.DC.	T	T	
<i>Wahlenbergia patula</i>	A.DC.	T	T	
<i>Wahlenbergia prostrata</i>	A.DC.	T	T	
Campanulaceae 110554		T	T	
<b>Capparaceae</b>				
<i>Boscia albitrunca</i>	(Burch.) Gilg & Gilg-Ben.	P	MiP/NP	
<i>Boscia foetida</i>	Schinz	P	MiP/NP	
<i>Cadaba aphylla</i>	(Thunb.) Wild	P	NP L red	
<i>Cleome foliosa</i>	Hook.f.	T	T/H	
<i>Cleome semitetrandra</i>	Sond.	T	T/H	
<i>Maerua gilgii</i>	Schinz	P	NP	
<i>Maerua schinzii</i>	Pax	C	Mi-Ch	
<b>Caryophyllaceae</b>				
<i>Dianthus namaensis</i>	Schinz	H	H	
<b>Celastraceae</b>				
<i>Maytenus linearis</i>	(L.f.) Marais	P	NP S rut	
<b>Chenopodiaceae</b>				
<i>Atriplex eardleyae</i>	Aellen	T	T	
<i>Manochiamys albicans</i>	(Aiton) Aellen	T	T	
<i>Salsola tuberculata</i>	(Moq.) Fenzl	C	M-Ch S frut L su per nan	
<i>Salsola zeyheri</i>	(Moq.) Bunge	C	M-Ch S frut L su per nan	
<i>Suaeda fruticosa</i>	(L.) Forssk.	C	M-Ch S frut L su per nan	
<b>Compositae</b>				
<i>Amellus epaleaceus</i>	O.Hoffm.	T	T/H	
<i>Amellus nanus</i>	DC.	T	T	
<i>Arctotis auriculata</i>	Jacq.	T	T	
<i>Arctotis fastuosa</i>	Jacq.	T	T	
<i>Berkheya canescens</i>	DC.	C	M-Ch th	
<i>Berkheya fruticosa</i>	(L.) Ehrh.	C	M-Ch th	
<i>Berkheya spinosissima s. namaensis v. argent</i>	(Thunb.) Willd. ssp. namaensis Roesler	C	M-Ch th	
<i>Chrysanthemoides incana</i>	(Burm.f.) Norl.	C	M-Ch	
<i>Chrysocoma ciliata</i>	E.Mey.	C	M-Ch	
<i>Chrysocoma oblongifolia</i>	DC.	C	M-Ch	Chrysocoma ciliata
<i>Chrysocoma puberula</i>	Merxm.	H	M-Ch	
<i>Chrysocoma schlechteri</i>	Ehr.Bayer	C	M-Ch	
<i>Dicoma capensis</i>	Less.	T	T S rept	
<i>Didelta carnosia v. carnosia</i>	(L.f.) Aiton	T	T L subsu	
<i>Didelta carnosia v. tomentosa</i>	(L.f.) Aiton (Less.) Roesler	T	T L subsu	
<i>Didelta spinosa</i>	(L.f.) Aiton	P	NP L subsu	
<i>Dimorphotheca acutifolia</i>	Hutch.	T	T	
<i>Dimorphotheca pluvialis</i>	(L.) Moench	T	T	Osteospermum acutifolium
<i>Dimorphotheca polyptera</i>	DC.	T	T	
<i>Dimorphotheca sinuata</i>	DC.	T	T	
<i>Elytropappus rhinocerotis</i>	(L.f.) Less.	C	M-Ch/NP	
<i>Eriocephalus africanus</i>	L.	C	M-Ch/NP L nan	
<i>Eriocephalus africanus s. paniculatus</i>		C	M-Ch/NP L nan	
<i>Eriocephalus ericoides</i>	(L.f.) Druce	C	M-Ch/NP L nan	
<i>Eriocephalus scariosus</i>	DC.	C	M-Ch	
<i>Euryops dregeanus</i>	Sch.Bip.	C	M-Ch	
<i>Euryops lateriflorus</i>	(L.f.) DC.	C	M-Ch	
<i>Euryops multifidus</i>	(Thunb.) DC.	C	M-Ch	
<i>Euryops namibensis</i>	(Merxm.) B.Nord.	C	M-Ch	
<i>Euryops subcamosus s. vulgaris</i>	DC. B.Nord.	C	M-Ch	
<i>Euryops tenuissimus s. tenuissimus</i>	(L.) DC.	C	M-Ch	
<i>Felicia filifolia s. schaeferi</i>	(Vent.) Burtt Davy (Dinter) Grau	C	M-Ch	
<i>Felicia ovata</i>	(Thunb.) Compton	C	M-Ch	
<i>Felicia scabrida</i>	(DC.) Range	T	T	
<i>Gazania lichtensteinii</i>	Less.	T	T	
<i>Gazania tenuifolia</i>	Less.	T	T	
<i>Geigeria vigintiquamea</i>	O.Hoffm.	T	T	
<i>Gorteria diffusa</i>	Thunb.	T	T	
<i>Helichrysum arenicola</i>	M.D.Hend.	T	T	
<i>Helichrysum hebelapis</i>	DC.	H	M-Ch	
<i>Helichrysum herniarioides</i>	DC.	T	T	
<i>Helichrysum leontonyx</i>	DC.	H	H	
<i>Helichrysum lucilioides</i>	Less.	C	M-Ch	
<i>Helichrysum micropoides</i>	DC.	H	H	
<i>Helichrysum obtusum</i>	(S.Moore) Moeser	T	T/N-Ch	
<i>Helichrysum revolutum</i>	(Thunb.) Less.	C	M-Ch	
<i>Helichrysum roseo-niveum</i>	Marloth & O.Hoffm.	T	T	
<i>Kleinia longiflora</i>	DC.	P	NP S lept L red	Senecio longiflorus
<i>Leysera tenella</i>	DC.	T	T	
<i>Oncosiphon grandiflorum</i>	(Thunb.) Källersjö	T	T	Pentzia grandiflora
<i>Oncosiphon piuliferum</i>	(L.f.) Källersjö	T	T	Pentzia piulifera
<i>Oncosiphon suffruticosum</i>	(L.) Källersjö	T	T	Pentzia suffruticosa
<i>Osteospermum armatum</i>	Norl.	C	M-Ch L subsu	

A. 12: Species list of the northern Richtersveld flora (cont.)

Species	Authority	LF	GF	Synonym
Osteospermum karrooicum	(Bolus) Norl.	T	T	
Osteospermum pinnatum	(Thunb.) Norl.	T	T	
Othonna abrotanifolia	(Harv.) Druce	C	M-Ch S lept L su ann	
Othonna amplexifolia	DC.	C	M-Ch L su	
Othonna arborescens		C	M-Ch L su	
Othonna arbuscula	(Thunb.) Sch.Bip.	C	M-Ch S lept L su ann	
Othonna clavifolia	Marloth	C	M-Ch L su	
Othonna cylindrica	(Lam.) DC.	C	M-Ch S lept L su ann per	
Othonna floribunda	Schltr.	C	M-Ch L su	
Othonna furcata	(Lindl.) Druce	P	NP S lept L su ann	
Othonna herrii	Pillans	C	N-Ch	
Othonna opima	Merxm.	C	M-Ch S lept L su per	
Othonna sedifolia	DC.	C	M-Ch S lept L su ann per	
Pegolettia retrofracta	(Thunb.) Kies	C	M-Ch	
Pentzia incana	(Thunb.) Kuntze	C	M-Ch	
Pentzia spinescens	Less.	C	M-Ch th	
Pteronia ciliata	Thunb.	C	M-Ch S frut L subsu	
Pteronia divaricata	(P.J.Bergius) Less.	C	M-Ch S frut L subsu ann per	
Pteronia glabrata	DC. Thunb.	C	M-Ch S frut L subsu ann per	Pteronia glauca
Pteronia glauca	Thunb.	C	M-Ch S frut L nan	
Pteronia lucilioides	DC.	P	NP S rut	
Pteronia onobromoides	DC.	C	M-Ch S frut	
Rhynchosidium pumilum	(L.f.) DC.	T	T	Reihania pumila
Rosenia glandulosa	Thunb.	C	M-Ch	
Rosenia oppositifolia	(DC.) K.Bremer	C	M-Ch	
Senecio aloides	DC.	C	T	
Senecio arenarius	Thunb.	T	T	
Senecio burchellii	DC.	T	T	
Senecio cardaminifolius	DC.	T	T	
Senecio corymbiferus	DC.	C	M-Ch S lept L su per	
Senecio maydae	Merxm.	C	M-Ch	
Senecio piptocoma	O.Hoffm.	T	T L subsu	
Senecio sisymbriifolius	DC.	T	T	
Trichogyne paronychioides	DC.	T	T S	Ifigia paronychioides
Tripteris brevibradiata	(Norl.) B.Nord.	T	T/Ch S L subsu	Osteospermum brevibradiatum
Tripteris microcarpa	(Harv.) Norl.	T	T/Ch S L su ann per	Tripteris microcarpa
Tripteris oppositifolia	(Aiton) B.Nord.	C	M-Ch S L su ann per	Osteospermum oppositifolium
Tripteris polyccephala	DC.	T	T/Ch S	Osteospermum polyccephalum
Tripteris sinuata	(DC.) Norl.	P	NP S L subsu	Osteospermum sinuatum
Ursinia cakilefolia	DC.	T	T	
Ursinia catenduliflora	(DC.) N.E.Br.	T	T	
Compositae 106517		T	T	
Compositae 108668		T	T	
<b>Crassulaceae</b>				
Adromischus alstonii	(Schönland & Baker f.) C.A.Sm.	C	Mi-Ch S frut L su per	
Adromischus filicaulis s. filicaulis	(Eckl. & Zeyh.) C.A.Sm.	C	N-Ch S frut L su per	
Adromischus marianiae	(Marloth) A.Berger	C	M-Ch L su per	
Cotyledon orbiculata v. orbiculata	L.	C	M-Ch S frut L su per	
Crassula atropurpurea v. cultiriformis	(Haw.) D.Dietr (Friedrich) Toelken	C	N-Ch L su per	
Crassula atropurpurea var. watermeyeri		C	N-Ch L su per	
Crassula barbata	Thunb.	C	Mi-Ch L su per	
Crassula brevifolia	(Eckl. & Zeyh.) Schönland	C	M-Ch S frut L su per	
Crassula columella	Marloth & Schönland	C	Mi-Ch L su per	
Crassula decumbens v. brachyphylla	Thunb. (Adamson) Toelken	C	Mi-Ch L su per	Crassula brevifolia
Crassula elegans s. elegans	Schönland & Baker f. ssp. elegans	C	N-Ch L su per	
Crassula expansa	Dryand.	C	Mi-Ch L su ann per	
Crassula grisea	Schönland	C	N-Ch L su per	
Crassula macowaniana	Schönland & Baker f.	C	M-Ch S frut L su per	
Crassula muscosa v. muscosa	L.	C	M-Ch S frut L su per nan	
Crassula muscosa v. obtusifolia	L. (Harv.) G.D.Rowley	C	M-Ch S frut L su per nan	
Crassula muscosa v. rigida	L. Toelken	C	M-Ch S frut L su per nan	Crassula muscosa v. obtusifolia
Crassula pseudohemisphaerica	Friedrich	C	N-Ch L su per	
Crassula rupestris	Thunb.	C	M-Ch S frut L su per	
Crassula S. Glabulea		C	M-Ch L su per	
Crassula S. Petrogenata		C	M-Ch L su per	
Crassula S. Rosularis		C	M-Ch L su per	
Crassula sericea	Schönland	C	N-Ch L su per	
Crassula sericea v. sericea	Schönland	C	N-Ch L su per	
Crassula sladenii	Schönland	C	M-Ch L su per	
Crassula species		C	M-Ch L su per	
Crassula subacaulis s. erosula	Schönland & Baker (N.E.Br.) Toelken	C	Mi-Ch L su per	
Crassula subaphylla	(Eckl. & Zeyh.) Harv.	C	Mi-Ch S frut L su per	
Crassula 106419		C	Mi-Ch L su ann per	
Crassula 106433		C	Mi-Ch L su ann per	
Crassula 106994		C	Mi-Ch L su ann per	
Crassula 108717		C	Mi-Ch L su ann per	
Crassula 108944		C	Mi-Ch L su ann per	
Crassula 109213		C	Mi-Ch L su ann per	
Crassula 109488		C	Mi-Ch L su ann per	
Tillaea 106446		C	Mi-Ch L su per	
Tylecodon buchholzianus	(Schuldt & Stephens) Toelken	C	M-Ch S L su ann	
Tylecodon hallii	(Toelken) Toelken	C	M-Ch S L su ann	
Tylecodon paniculatus	(L.f.) Toelken	P	NP S pach L su ann	
Tylecodon racemosus	(Harv.) Toelken	P	NP S pach L su ann	
Tylecodon reticulatus	(L.f.) Toelken	C	M-Ch S pach L su ann th	
Tylecodon rubrovenosus	(Dinter) Toelken	C	M-Ch S L su ann	
Tylecodon wallichii s. ecklonianus	(Harv.) Toelken	C	M-Ch S L su ann	
Tylecodon wallichii s. wallichii	(Harv.) Toelken	C	M-Ch S L su ann	
<b>Cruciferae</b>				
Heliophila camosa	(Thunb.) Steud.	T	T	
Heliophila cornuta v. squamata	Sond. (Schltr.) Marais	C	T	
Heliophila coronopifolia	L.	T	T	
Heliophila deserticola	Schltr.	T	T	
Heliophila trifurca	Burch. ex DC.	T	T	
Heliophila variabilis	Burch. ex DC.	T	T	
<b>Cucurbitaceae</b>				
Cucumis africanus	L.f.	T	T	
Cucumis meeusei	C.Jeffrey	T	T	
Cucumis rigidus	E.Mey. ex Naudin	T	T/H	
Kedrostis psammophylla	Bruyns	H	H	
Kedrostis species				

## A. 12: Species list of the northern Richtersveld flora (cont.)

Species	Authority	LF	GF	Synonym
<b>Ebenaceae</b>				
Diospyros ramulosa	(E.Mey. ex A.DC.) De Winter	C	NP	
Euclea pseudebenus	E.Mey. ex A.DC.	P	MiP/NP	
<b>Euphorbiaceae</b>				
Euphorbia brachiata	E.Mey. ex Boiss.	C	Mi-Ch S lept L red	
Euphorbia chersina	N.E.Br.	C	M-Ch S rut lept L red	
Euphorbia decussata	E.Mey. ex Boiss.	C	M-Ch S rut lept L red	
Euphorbia dregeana	E.Mey. ex Boiss.	P	NP S rut lept L red	
Euphorbia ephedroides	E.Mey. ex Boiss.	C	M-Ch S rut lept L red	
Euphorbia francescae	L.C.Leach	P	M-Ch r suc	
Euphorbia gariepina	Boiss.	C	M-Ch S pach L red	
Euphorbia guerichiana	Pax	P	NP S fruit	
Euphorbia gummifera	Boiss.	P	NP S rut lept L red	
Euphorbia hamata	(Haw.) Sweet	C	M-Ch S pach L red	
Euphorbia mauritanica Gariep		P	NP S rut lept L red	
Euphorbia mauritanica v. corallothamnus	L. Dinter ex A.C.White, R.A.Dyer & B.Sloane	P	NP S rut lept L red	
Euphorbia mauritanica v. foetens	L.	P	NP S rut lept L red	
Euphorbia mauritanica v. mauritanica	L.	P	NP S rut lept L red	
Euphorbia phylloclada	Boiss.	T	T	
Euphorbia spinea	N.E.Br.	C	M-Ch S rut lept L red	
Euphorbia stapelioides	Boiss.	C	Mi-Ch S lept L red	
Euphorbia tuberculata	Jacq.	C	M-Ch S lept L red	
Euphorbia virosa	Willd.	P	NP S pach L red	
Ricinus communis	L.	P	NP	
<b>Geraniaceae</b>				
Monsonia luederitziana	Focke & Schinz	T	T/H	
Monsonia parvifolia	Schinz	T	T	
Pelargonium antidysentericum	(Eckl. & Zeyh.) Kostel.	C	M-Ch S L ann	
Pelargonium articulatum	(Cav.) Willd.	C	M-Ch	
Pelargonium carnosum	(L.)L'Hér.	C	M-Ch	
Pelargonium ceratophyllum	L'Hér.	C	M-Ch S pach L su ann	
Pelargonium crassicaule	L'Hér.	C	M-Ch S L ann	
Pelargonium crithmifolium	Sm.	C	M-Ch S pach L subsu ann th	
Pelargonium dasyphyllum	E.Mey. ex R.Knuth	C	M-Ch	
Pelargonium desertorum	Vorster	C	M-Ch S L ann	
Pelargonium echinatum	Curtis	C	M-Ch S pach L ann	
Pelargonium Klinghardtense	R.Knuth	C	M-Ch S pach L su ann	
Pelargonium praemorsum s. speciosum	(Andrews) F.Dietr. Scheltema	C	M-Ch S L ann	
Pelargonium species				
Pelargonium spinosum	Willd.	C	M-Ch S L subsu ann	
Pelargonium tenuicaule	R.Knuth	C	M-Ch S L subsu ann	
Sarcocaulon crassicaule	crassicaule Rehm	C	N-Ch S L ann	
Sarcocaulon patersonii	(DC.) G.Don	C	N-Ch S L ann	
<b>Gisekiaceae</b>				
Gisekia pharnacioides	L.	T	T/H	
<b>Hydrophyllaceae</b>				
Codon royenii	L.	C	M-Ch	
<b>Labiatae</b>				
Acrotome pallescens	Benth.	C	M-Ch	
Ballota africana	(L.) Benth.	C	M-Ch	
Salvia garipensis	E.Mey. ex Benth.	C	NP/M-Ch	
Stachys lamarckii	Benth.	T	M-Ch	
<b>Leguminosae</b>				
<b>Caesalpinioideae</b>				
Adenolobus garipensis	(E.Mey.) Torre & Hillc.	P	MiP	
Parkinsonia africana	Sond.	P	MiP	
Schotia afra	(L.) Thunb.	P	MiP	
<b>Mimosoideae</b>				
Acacia karroo	Hayne	P	MiP	
Prosopis glandulosa	Torr.	P	MiP	
<b>Papilionoideae</b>				
Crotalaria humilis	Eckl. & Zeyh.	C	M-Ch	
Crotalaria meyeriana	Steud.	C	M-Ch	
Indigostrum argyroides	(E.Mey.) Schrire	T	T	Indigofera argyroides
Indigofera exigua	Eckl. & Zeyh.	C	Mi-Ch	
Indigofera nigromontana	Eckl. & Zeyh.	C	M-Ch	Indigofera spinescens
Indigofera pungens	E.Mey.	C	M-Ch	
Indigofera sp. nov. 22906		C	M-Ch	
Lebeckia cinerea	E.Mey.	P	NP	
Lebeckia multiflora	E.Mey.	P	NP	
Lebeckia sericea	Thunb.	P	NP	
Lessertia inflata	Harv.	C	M-Ch	
Lessertia spinescens	E.Mey.	C	M-Ch	
Lotononis falcata	(E.Mey.) Benth.	T	T	
Lotononis strigillosa	(Merxm. & A.Schreib.) A.Schreib.	T	T	
Rhynchosia emarginata	Germish.	C	M-Ch	
Sutherlandia frutescens	(L.) R.Br.	H	H S rept	
Tephrosia dregeana	E.Mey.	C	M-Ch	
<b>Loasaceae</b>				
Kissenia capensis	Endl.	T	T	
<b>Malvaceae</b>				
Abutilon pycnodon	Hochr.	H	H	



Species	Authority	LF	GF	Synonym
<b>Meliaceae</b>				
Nymanina capensis	(Thunb.) Lindb.	P	NP	AITONIACEAE
<b>Melanthaceae</b>				
Melianthus pectinatus	Harv.	P	NP	
<b>Menispermaceae</b>				
Antizoma miersiana	Harv.	C	NP/Ch	
<b>Molluginaceae</b>				
Adenogramma glomerata	(L.f.) Druce	T	T L su	
Coelanthum grandiflorum	E.Mey. ex Fenzl	C	Mi-Ch	
Hypertelis sauloides	(Burch.) Adamson	C	Mi-Ch S frut L su per	
Lineum aethiopicum	Burm.	T	T/H	
Lineum fenestratum v. fenestratum	(Fenzl) Heimerl	T	T/H	
Phamaceum alpinum	Adamson	T	T	
Phamaceum croceum	E.Mey. ex Fenzl	T	T	
Phamaceum exiguum	Adamson	T	T	
<b>Montiniaceae</b>				
Montinia caryophyllacea	Thunb.	P	NP	
<b>Moraceae</b>				
Ficus ilicina	(Sond.) Miq.	P	MiP	
<b>Neuradaceae</b>				
Grielum grandiflorum	(L.) Druce	C	H/T S rept r suc	
Grielum humifusum	Thunb.	C	H/T S rept r suc	
<b>Oleaceae</b>				
Menodora juncea	Harv.	C	M-Ch	
<b>Oxalidaceae</b>				
Oxalis beneprotecta	Dinter ex R.Knuth	G	G	Oxalis bullulata
Oxalis cathara	Salter	G	G	
Oxalis pardalis	Sond.	G	G	Oxalis massoniana
Oxalis pes-caprae	L.	G	G	
Oxalis species		G	G	
<b>Pedaliaceae</b>				
Rogeria longiflora	(Royer) J.Gay ex DC.	T	T	
<b>Plantaginaceae</b>				
Plantago cafra	Decne.	T	T	
<b>Plumbaginaceae</b>				
Dyerophytum africanum	(Lam.) Kuntze	P	NP S rut	
Limonium dyeri	Lincz.	C	M-Ch	
<b>Polygalaceae</b>				
Polygala virgata	Thunb.	C	M-Ch S frut	
<b>Portulacaceae</b>				
Anacamperos species		C	N-Ch	
Avonia albissima	(Marloth) G.D.Rowley	C	Mi-Ch L red	
Ceraria fruticulosa	H.Pearson & Stephens	C	M-Ch/NP S L su ann	
Ceraria namaquensis	(Sond.) H.Pearson & Stephens	P	NP S L su ann nan	
Portulacaria pygmaea	Pillans	P	NP	
<b>Resedaceae</b>				
Oligomeris dipetala	(Aiton) Turcz.	C	Mi-Ch	
<b>Rhamnaceae</b>				
Ziziphus mucronata	Willd.	P	MiP	
<b>Rubiaceae</b>				
Crocylis anthospermoides	E.Mey. ex K.Schum.		M-Ch	
Gaillonia crocylis	(Sond.) Thulin	C	M-Ch	Crocylis anthospermoides
Kohautia cynanchica	DC.	T	T	
<b>Santalaceae</b>				
Thesium congestum	R.A.Dyer	C	M-Ch S rut	
Thesium elatius	Sond.	C	M-Ch	
Thesium lineatum	L.f.	C	M-Ch/NP S rut	
Thesium strictum	P.J.Bergius	C	M-Ch S rut	
<b>Sapindaceae</b>				
Dodonaea angustifolia	L.f.	P	NP	
<b>Scrophulariaceae</b>				
Aptosimum spinescens	(Thunb.) Weber	C	Mi-Ch	
Aptosimum suberosum	Weber	C	Mi-Ch	
Hebenstretia parviflora	E.Mey.	T	T	

A. 12: Species list of the northern Richtersveld flora (cont.)

Species	Authority	LF	GF	Synonym
Hemimeris racemosa	(Houtt.) Merr.	T	T	
Hiernia species	Hiernia species			
Jamesbrittenia atropurpurea	(Benth.) Hilliard	C	M-Ch	
Jamesbrittenia fruticosa	(Benth.) Hilliard	C	M-Ch	Sutera fruticosa
Jamesbrittenia glutinosa	(Benth.) Hilliard	C	M-Ch	
Jamesbrittenia maritima	(Hiern) Hilliard	C	Mi-Ch	
Jamesbrittenia ramosissima	(Hiern) Hilliard	T	T	Sutera ramosissima
Jamesbrittenia 110558		C	M-Ch	
Lyperia tristis	(L.f.) Benth.	T	T	Sutera tristis
Manulea corymbosa	L.f.	T	T	Manulea benthamiana
Nemesia bicornis	(L.) Pers.	T	T	
Nemesia ligulata	E.Mey. ex Benth.	T	T	
Nemesia species nov.	Nemesia species	T	T	
Nemesia viscosa	E.Mey. ex Benth.	T	T	
Nemesia 106338		T	T	
Nemesia 108706		T	T	
Pelostomum leucorrhizum	E.Mey. ex Benth.	C	Mi-Ch	
Pelostomum virgatum	E.Mey. ex Benth.	C	Mi-Ch	
Pelostomum viscosum	E.Mey. ex Benth.	T	T	
Polycarena pumila	Levyns	T	T	Phyllopodium pumilum
Polycarena selagenoides	Schltr. Ex Hiern	T	T	
Selago albida	Choisy	C	M-Ch	
Selago divaricata	L.f.	C	M-Ch	Selago minutissima
Selago robusta	Rolfe	C	M-Ch	
Sutera ramosissima	Hiern(Hiern) Hilliard	T	T	
Sutera squarrosa	(Pilg.) Hiern ex Range	T	T	
Sutera tomentosa	(Thunb.) Hiern	T	T	
Zaluzianskya affinis	Hilliard	T	T	
<b>Solanaceae</b>				
Lycium cinereum	Thunb. sensu lato	C	M-Ch S frut	
Lycium ferocissimum	Miers	C	M-Ch S frut L su	
Lycium hirsutum	Dunal	C	M-Ch S frut	
Lycium oxycarpum	Dunal	C	M-Ch S frut	Lycium austrinum
Lycium species		C	M-Ch S frut	
Lycium 109185		C	M-Ch	
Nicotiana glauca	Graham	P	MIP	
Solanum burchellii	Dunal	C	M-Ch	
<b>Sterculiaceae</b>				
Hermannia althaeifolia	L.	C	M-Ch	
Hermannia amoena	Dinter ex Friedr.-Holzh.	C	M-Ch	
Hermannia cuneifolia	Jacq.	C	M-Ch	
Hermannia disermifolia	Jacq.	C	M-Ch	
Hermannia ganepina	Eckl. & Zeyh.	C	M-Ch	
Hermannia paucifolia	Turcz.	C	M-Ch	
Hermannia scabra	Cav.	C	M-Ch	
Hermannia stricta	(E.Mey. ex Turcz.) Harv.	C	M-Ch	
Hermannia trifurca	L.	C	M-Ch	
<b>Tamaricaceae</b>				
Tamarix usneoides	E. Mey. ex Bunge	P	MIP	
<b>Umbelliferae</b>				
Annesorhiza 106438		T	T	
Annesorhiza 108663		T	T	
Sonderina tenuis	(Sond.) H.Wolff	T	T/H	
<b>Urticaceae</b>				
Forsskaolea candida	L.f.	H	H/Ch	
Forsskaolea oiridis		T	T	
<b>Zygophyllaceae</b>				
Augea capensis	Thunb.	C	M-Ch L su ann	
Fagonia capensis	Hadidi	C	Mi-Ch	
Sisyndite spartea	E.Mey. ex Sond.	P	NP S frut	
Tribulus terrestris	L.	T	T S rept	
Tribulus zeyheri	Sond.	T	T S rept	
Zygophyllum clavatum	Schltr. & Diels	C	M-Ch S frut L su ann per	
Zygophyllum cordifolium	L.f.	C	Mi-Ch S frut L su ann per	
Zygophyllum cordifolium fine		C	M-Ch S frut L su ann per	
Zygophyllum decumbens	Dellile	C	M-Ch S frut L su ann per	
Zygophyllum dregeanum	Sond.	C	M-Ch S frut L su ann per	
Zygophyllum flexuosum	Eckl. & Zeyh.	C	M-Ch S frut L su ann per	
Zygophyllum foetidum	Schrad. & J.C.Wendl.	C	M-Ch S frut L su ann per	
Zygophyllum leptopetalum	E.Mey. ex Sond.	C	M-Ch S frut L su ann per	
Zygophyllum macrocarpon	Retief	C	M-Ch S frut L su ann per	
Zygophyllum microcarpon	Licht. ex Cham. & Schldl.	C	M-Ch S frut L su ann per	
Zygophyllum microphyllum	L.f.	C	M-Ch S frut L su ann per	
Zygophyllum morgsana	L.	P	NP S frut L su ann per	
Zygophyllum patenticaulae	Van Zyl, sp. nov.	C	Mi-Ch S frut L subsu ann	Zygophyllum prismatocarpum CH
Zygophyllum prismatocarpum	E.Mey. ex Sond.	P	NP/MIP S frut L su ann per	Zygophyllum prismatocarpum NP
Zygophyllum retrofractum	Thunb.	C	M-Ch S frut L su ann per	
Zygophyllum spinosum	L.	C	Mi-Ch S frut L su ann per	
<b>Indet.</b>				
Genspec 106386				
Genspec 106445				
Genspec 106487				
Genspec 108611				
Genspec 108659				
Genspec 108749				
Genspec 108414				
Genspec 3835				
Genspec 3846				

A. 12: Species list of the northern Richtersveld flora (cont.)















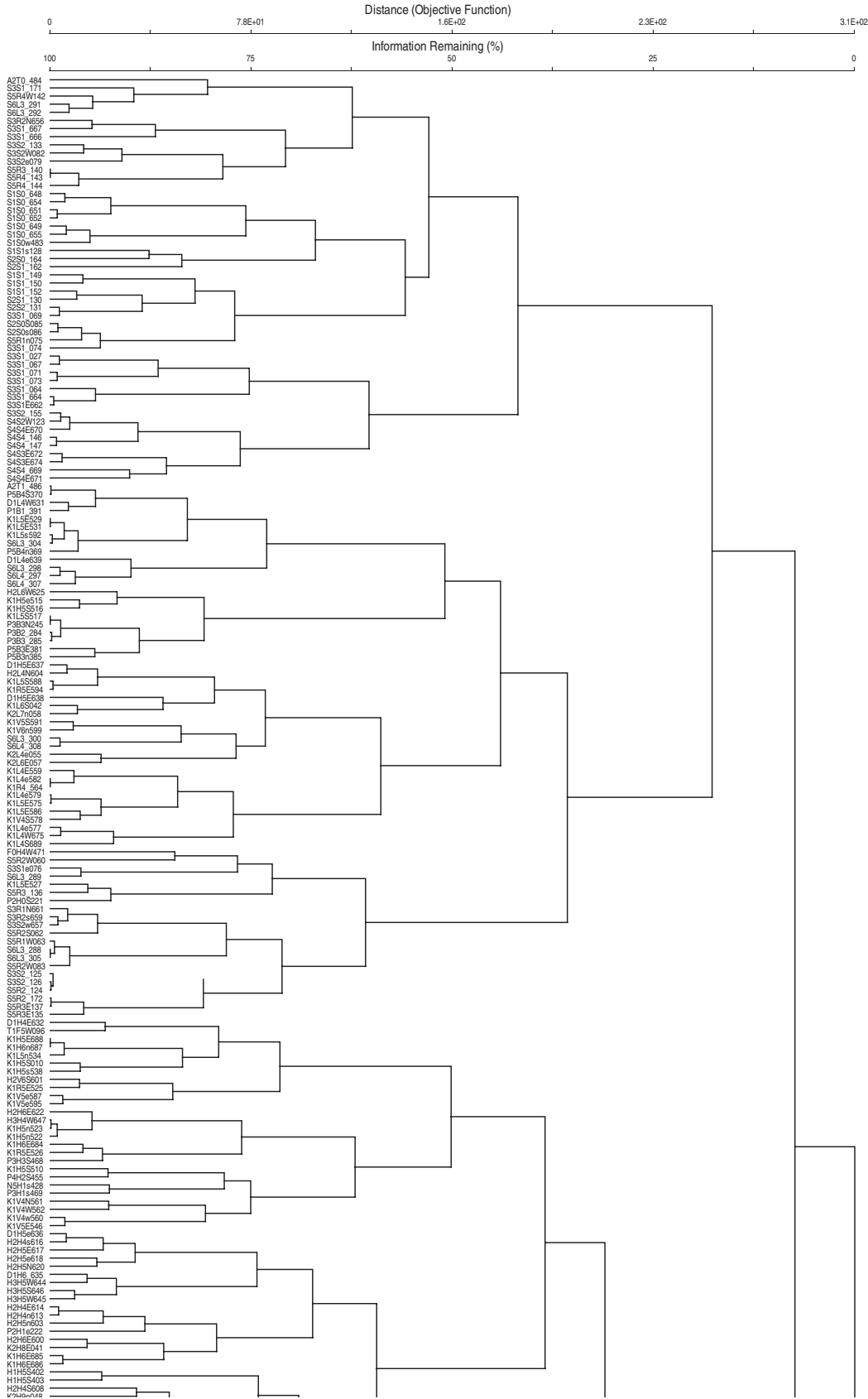




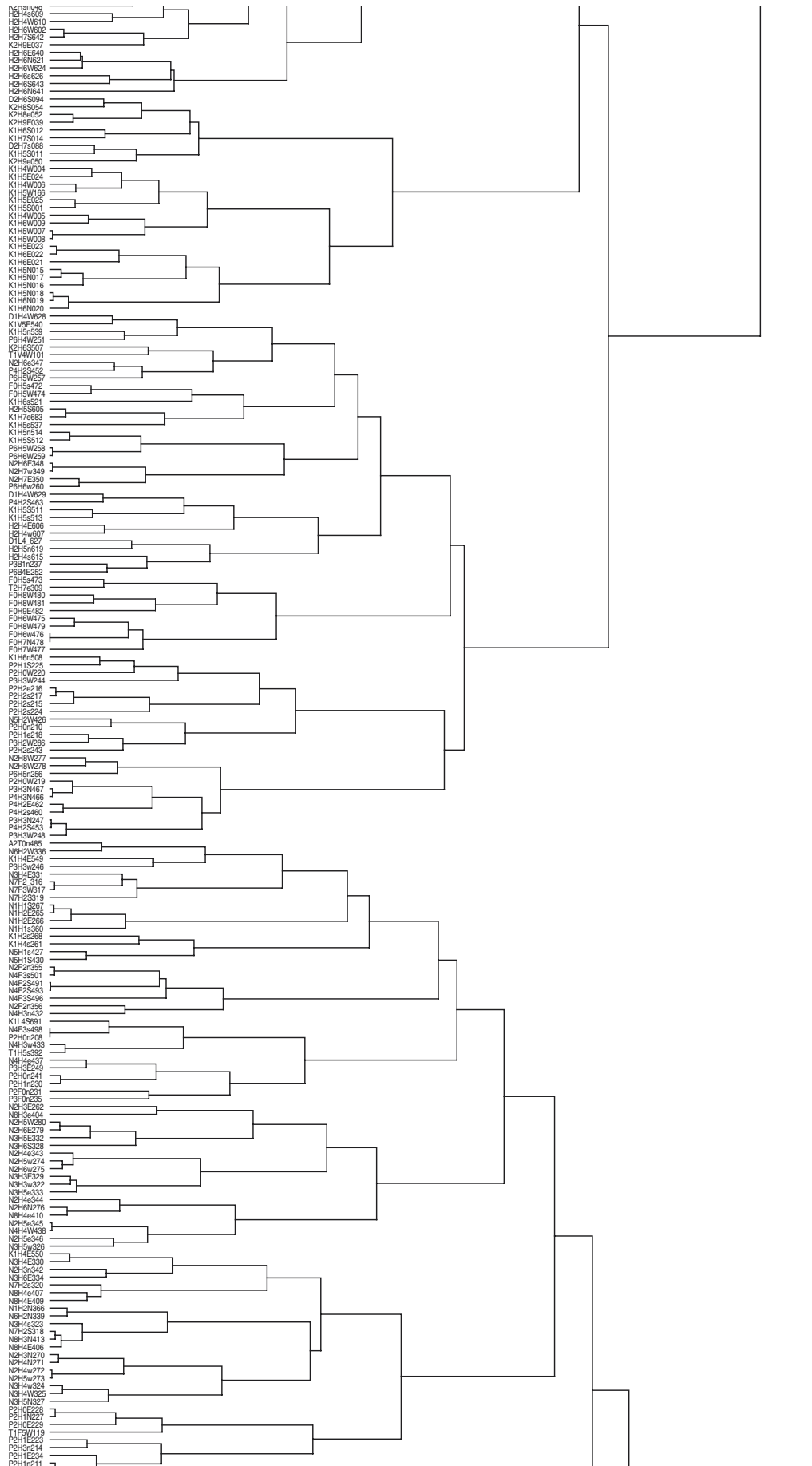




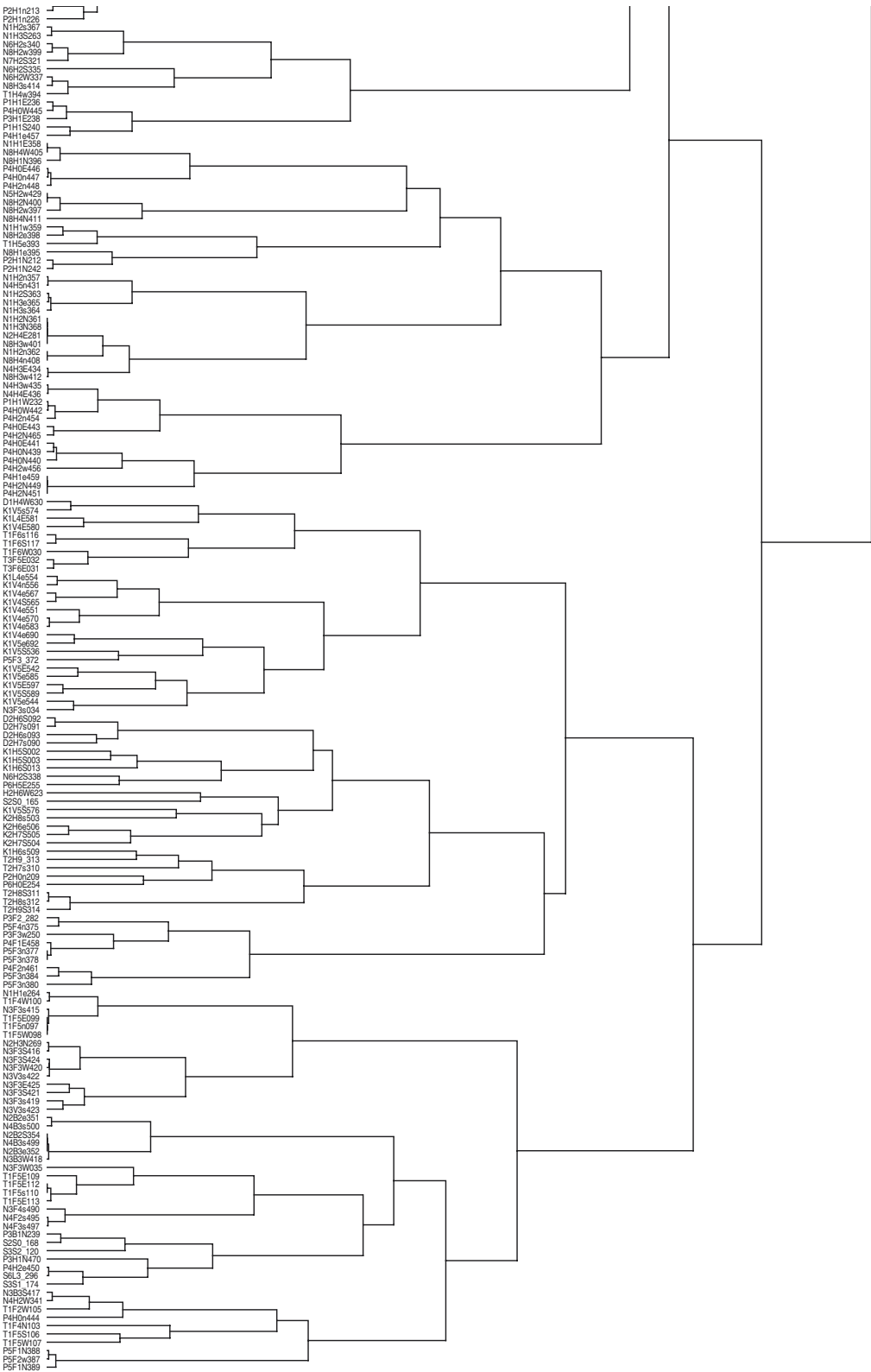
A. T1: Cluster analysis (515 relevés, 403 species; Sørensen index, Flexible beta -5)



A. T1: Cluster analysis



A. T1: Cluster analysis (cont.)



A. T1: Cluster analysis (cont.)

A. T2

C = Consistency within the table
Owg = Consistency within the group
Cwg = Consistency outside the group

Table with columns: V1, V2, V3, V4, V5, V6, LF, SPEC, No Z, COW, VZ, S1, S2, S3, S4, CLUSTER, HINDEX, EVENESS, SPEC, No Z, COW, VZ, S1, S2, S3, S4, EAST, WEST, S, N, W, C, C%, CI, C%, Owg, Owg%, Cwg, Cwg%, GEO, and various species names. The table contains a large amount of data for various plant species, including Apargue capensis, Croxiphon suffruticosum, Euphorbia esula, etc.

















A. T6

C = Constancy
Ct = Constancy within the table
Cwg = Constancy within the group
Cog = Constancy outside the group

Table with columns for V1-V6, LF, Fst1-Fst6, Pgt1-Pgt6, C-CLUSTER, H-INDEX, SPEC No, COV10, and various plant species names. Includes a detailed legend for C, Ct, Cwg, and Cog, and a large grid of numerical data for each species across different categories.



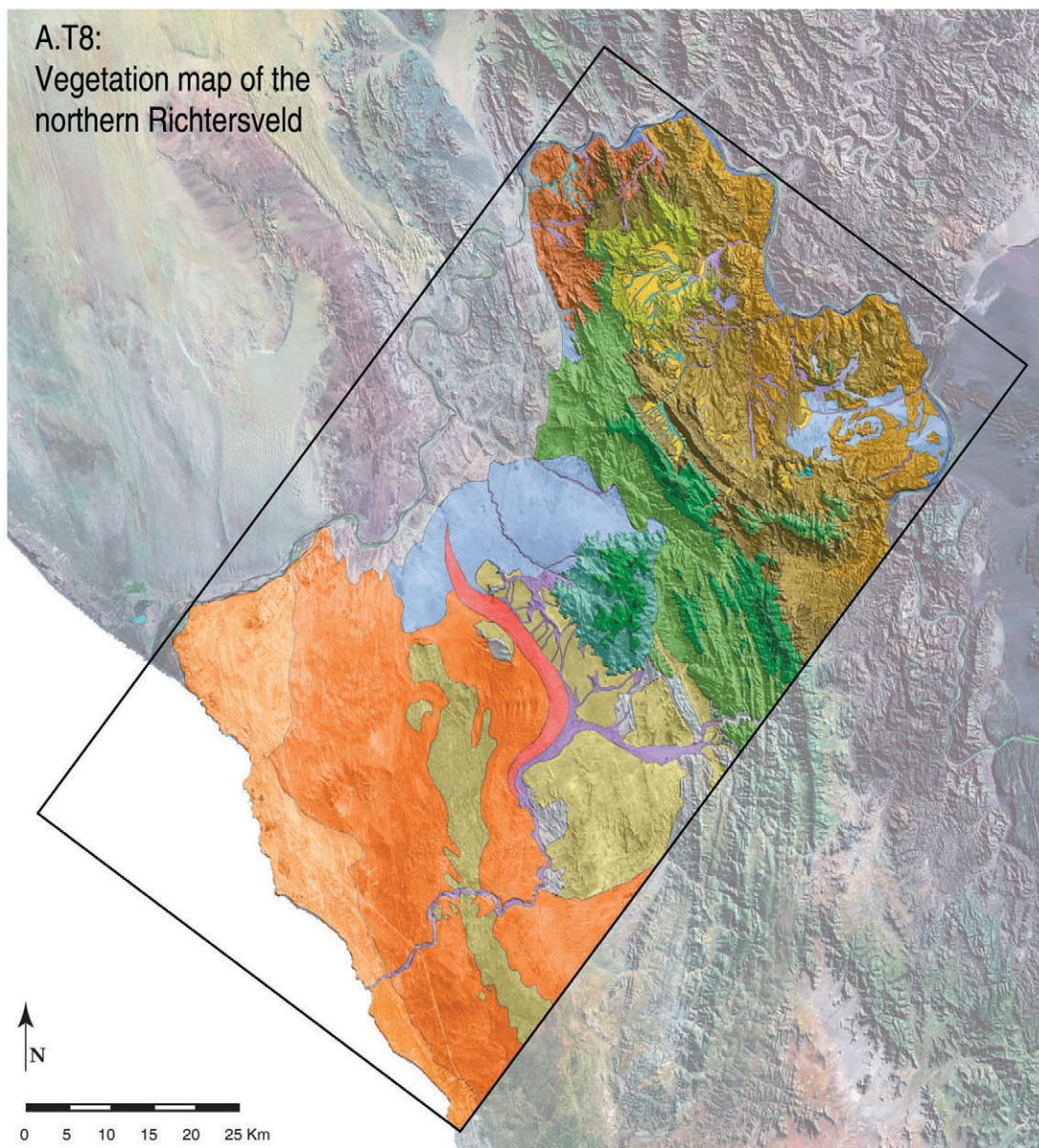












**Succulent Karoo**

**Sandy habitats of the coastal plain**

- *Zygophyllum clavatum* - *Euphorbia brachiata* ass. 1111
- *Zygophyllum morgsana* - *Hermannia trifurca* ass. 1112
- *Cladoraphis spinosa* - *Limeum fenestratum* sub-ass. 11122

**Silty habitats of the coastal plain and inner mountain basins**

- *Cheiridopsis robusta* - *Ruschia leucosperma* ass. 1121
- *Aridaria noctiflora* - *Trachyandra muricata* ass. 1122

**Habitats of the Orange River terraces**

- *Brownanthus pubescens* ass. 1131

**Slope habitats within the mountain area**

- *Elytropappus rhinocerotis* - *Merxmuellera dura* sub-ass. 12111
- *Pteronia divaricata* - *Berkheya canescens* sub-ass. 12112
- *Antizoma miersiana* - *Ruschia Tumidula* black fruits ass. 1212
- *Crassula grisea* - *Ruschia elineata* ass. 1213
- *Chrysocoma puberula* - *Menodroa juncea* all. 122

**Nama Karoo**

**Habitats of gravely flood plains and drainage lines**

- *Leucophrys mesocoma* - *Monechma mollissimum* ass. 2121
- *Monechma spartioides* - *Cadaba aphylla* ass. 2122
- *Prenia tetragonia* - *Psilocaloun subnodosum* ass. 2115
- *Sisyndite spartea* - *Rogeria longiflora* ass. 2114

**Open sand plains**

- *Stipagrostis obtusa* com. 3212

**Gallery forests along the Orange River banks**

- *Rhus pendulina* - *Ziziphus mucronata* com. 3102

**Slope habitats within the mountain area**

- *Pachypodium namaquanum* ass. 2211
- SW: *Acrotome pallescens* - *Astridia alba* ass. 1214, NE: *Zygophyllum microcarpum* ass. 2212
- S: *Brownanthus nucifer* - *Ruschia abbreviata* ass. 2213, N: *Euphorbia decussata* ass. 2214
- *Euphorbia virosa* - *Euphorbia gariepina* ass. 2215

## Zusammenfassung

Das artenreiche Richtersveld mit seiner außergewöhnlich schönen Landschaft steht im Konflikt verschiedener Nutzungsinteressen und ist durch zunehmenden Druck auf das Land in seinem ökologischen Wert gefährdet. Um ein angepasstes Management des Richtersveld Nationalparks zu garantieren, konzentriert sich ein Bereich der etablierten wissenschaftlichen Projekte auf die Beschreibung und Kartierung der heutigen Vegetation.

Hierfür wurde in der vorliegenden Arbeit eine pflanzensoziologische Gliederung der Vegetation des nördlichen Richtersveldes auf der Basis von über 800 Vegetationsaufnahmen erstellt. Eine grobe Unterteilung ist durch die fünf vorherrschenden Landschaftseinheiten gegeben. Die sandige Küstenebene und die schluffigen Ebenen und Hänge der Randstufe sind vorwiegend mit einer Zwergstrauchvegetation bedeckt. Auf den schluffigen Hängen des Oranjetals herrscht eine trockene Strauchvegetation vor, während die Schichtflutebenen und Trockentäler eine offene Strauchvegetation tragen. Die detaillierte Gliederung ergibt 23 Assoziationen verteilt auf vier Verbände der Sukkulente Karoo (*Kapflora*) und drei Verbände der Nama Karoo (*Paläotropis*).

Um die Faktoren zu erfassen, die die räumlichen Vegetationsmuster bestimmen, wurde der Einfluss des Klimas, der Geologie, des Reliefs und des Bodens auf die Vegetation untersucht. Die Klimavariablen mittlerer Jahresniederschlag im Winter und mittlere Maximumtemperatur im Sommer wurden als Haupteinflussgrößen erkannt, die die Vegetationsverbreitung auf regionaler Ebene determinieren. Der Boden gliedert über Karbonatgehalt, Skelettanteil und Bodenart vor allem die Vegetation auf den ebenen Standorten. Die Beschaffenheit der Gesteine beeinflusst die Vegetationsmuster indirekt über Bodenchemie und Standortgliederung. Lokal wirkt das Relief als bestimmender Faktor, zu erkennen an der Ausprägung eigener Assoziationen auf verschiedenen exponierten Hängen.

Die Hauptklimavariablen korrelieren negativ miteinander. Während der mittlere Jahresniederschlag im Winter mit niedrigsten Werten an der Atlantikküste zunächst mit dem Anstieg der Randstufe zunimmt, um dort die höchsten Werte zu erreichen, nimmt er stetig zum Oranjetal hin wieder ab. Hierzu gegenläufig verhält sich die mittlere Maximumtemperatur im Sommer. Die Vegetationsmuster verändern sich entlang dieses Klimagradienten vom Winterregen- zum angrenzenden Sommerregenregime. Es werden die Syntaxa der Sukkulente Karoo abgelöst von denen der Nama Karoo. Abundanz und Deckung der Arten nehmen ab - mit einem Maximum auf der Randstufe. Und der Anteil, der an die Küstenwüste gut angepassten, blattsukkulente Chamaephyten geht zurück. Hiermit ist ein zunehmendes Auftreten von Nanophanerophyten und Stammsukkulenz verbunden, das den klimatischen Wandel und damit den Übergang von Sukkulente Karoo zu Nama Karoo auf der Höhe des Oranjetals kennzeichnet.

Das extrazonale Vorkommen der hier seltenen Fynbos Elemente ist auf die Gipfel der Randstufe beschränkt.

Die in dieser Arbeit gewonnenen Erkenntnisse sind in einer Vegetationskarte festgehalten.

## **Abstract**

The ecologically valuable Richtersveld with its high biodiversity and exceptionally beautiful landscape is endangered by different and changing exploitation interests, which result in increased pressure on the land. In order to ensure suitable land management of the Richtersveld National Park, one of the established research projects focuses on the mapping and description of the present vegetation.

For this reason the study on hand set up a phytosociological classification for the northern Richtersveld on the basis of more than 800 vegetation relevés. Five basic landscape units subdivide the vegetation into the predominating dwarf shrub communities on the coastal sand plain, silty plains and slopes of the escarpment; the dry shrub communities on silty slopes of the eastern Gariep; and the open shrub communities on gravelly flood plains and drainage lines. The detailed division reveals 23 associations, within four alliances of the Succulent Karoo (*Greater Cape Flora*) and three alliances of the Nama Karoo (*Palaeotropis*).

In order to gain an insight into the extent of the environmental influence on the vegetation pattern the factors climate, geology, relief and soil were investigated. The climate variables, precipitation in winter and maximum air temperature in summer, are the dominant factors, which influence the vegetation spread on a regional scale. Soil texture, carbonate and stone content determine the associations on the plains. The mineral content and weathering of different geological units influences the vegetation indirectly via the soil properties and the structuring of the habitats. The decisive influence of the relief emerged on a local scale, which can mainly be observed in the appearance of separate associations on different slope aspects.

The main climatic variables correlate negatively. The precipitation amount in winter with the lowest values at the Atlantic Ocean increases with the ascent of the African plate, reaching the highest values at the top and decreases gently down to the Orange River valley. The mean maximum air temperature in summer follows a reverse trend. The vegetation pattern changes along this climatic gradient from the winter rainfall to the bordering summer rainfall regime. The syntaxa of the Succulent Karoo are replaced by those of the Nama Karoo and the species diversity as well as the canopy cover decreases with a peak on the escarpment. The decline of the climatically well-adapted leaf succulent chamaephytes, together with the appearance of stem succulents and phanerophytes, indicates the climatic change and therefore the transition from Succulent to Nama Karoo in the vicinity of the Orange River valley.

The extrazonal occurrence of the Fynbos elements is restricted to the summits of the escarpment.

A vegetation map reports the results of the study.



Ich versichere, daß ich die von mir vorgelegte Dissertation selbständig angefertigt, die benutzten Quellen und Hilfsmittel vollständig angegeben und die Stellen der Arbeit - einschließlich Tabellen, Karten und Abbildungen -, die anderen Werken im Wortlaut oder dem Sinn nach entnommen sind, in jedem Einzelfall als Entlehnung kenntlich gemacht habe; daß diese Dissertation noch keiner anderen Fakultät oder Universität zur Prüfung vorgelegen hat; daß sie - abgesehen von unten angegebenen Teilpublikationen - noch nicht veröffentlicht worden ist sowie, daß ich eine solche Veröffentlichung vor Abschluß des Promotionsverfahrens nicht vornehmen werde. Die Bestimmungen dieser Promotionsordnung sind mir bekannt. Die von mir vorgelegte Dissertation ist von Prof. Dr. M. Melkonian betreut worden. Es existieren keine Teilpublikationen.