OL

Desert

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N. Jürgens, A. Burke, M.K. Seely and K.M. Jacobson

9.1 Introduction

The desert biome of southern Africa (defined by Rutherford & Westfall 1986, but extended in this contribution) is represented almost exclusively by the Namib Desert. It covers 111 147 km^2 or 4.15% of the region discussed in this volume. The Namib has been the focus of much interest (Koch 1962; Werger 1978; Ward, Seely & Lancaster 1983; Walter & Breckle 1984; Walter 1986; Seely 1991; Jürgens 1991), as it is regarded as a very old desert (Ward & Corbett 1990) and possesses unique environmental conditions, unique adaptations and highly interesting biota including the monotypic gymnosperm *Welwitschia mirabilis* (Bornman 1972, 1977; Von Willert 1985). Nevertheless, no complete treatment of the vegetation of the Namib has been published hitherto. Only certain parts of the Namib, notably the vegetation of the dunes and plains of the central Namib in the vicinity of the desert research station at Gobabeb have been studied intensively, while other parts of this vast strip of land, nearly 2000 km long in a north-south direction (Ward *et al.* 1983), have been neglected. In this chapter we review both published data and unpublished studies throughout the Namib.

From many perspectives, there is not one Namib Desert, but two: one comprising the most arid portions of the succulent karoo biome, and the other the Nama-karoo biome. Because of the continuous transition between extreme desert and the more humid parts of the two adjacent biomes, some vegetation units are discussed in this desert chapter, which could just as well be included in the chapters on the succulent karoo biome (Chap. 7, this volume) or the Nama-karoo biome (Chap. 8, this volume) (for details see 9.3.1).

Landscapes in the Namib Desert range from areas devoid of any vegetation, to many areas where there is a relatively dense ground layer of herbs and dwarf shrubs with taller shrubs and even small trees – at least at sites with a slightly better water regime. Such a wide spectrum of habitats, ranging from 'extreme desert' to 'the edge of the savanna', is found in many deserts in the world. However, the Namib is special with respect to the rapid change of vegetation over short distances, owing to extremely steep ecological gradients. Over intervals of sometimes less than 100 km, the complete spectrum can be observed from succulent karoo biome shrubland through absolute desert to semi-desert with patches of savanna. Consequently the analysis of these steep ecological gradients and the related vegetation is essential for the understanding of desert vegetation.

9.2 Environmental gradients

Numerous environmental parameters of the Namib Desert co-vary in space and can be understood as parts of more general gradients (complex gradients; Walter 1971). Such general gradients are: tropical to temperate conditions along a north–south axis; and coastal to inland conditions along an east–west axis. Both gradients have a major influence on the flora and vegetation. The temperate–tropical gradient is gentle, whereas the coast–inland gradient is very steep. The southern extremity of the temperate–tropical gradient is represented by the temperate winter-rainfall region of the most arid parts of the succulent karoo biome, e.g. Namaqualand, Richtersveld, Ceres Karoo and the western parts of the Little Karoo. Here mild temperatures and higher relative humidity lead to relatively low potential evapotranspiration (Chap. 2, this volume). The northern extremity is represented by the tropical summer-rainfall region in arid northern Namibia and southwestern Angola, characterized by high temperatures, low humidity and high potential evapotranspiration.

The coast-inland gradient shows some similarities to the temperate-tropical gradient. Throughout the extent of the Namib coast, from Namaqualand to northern Namibia, almost identical climatic conditions prevail, characterized by mild temperatures, very high humidity and high fog incidence (Fig. 9.1*a*; Olivier 1995). In contrast, the inland conditions are characterized by much higher temperatures and lower humidity, but (in Namibia) higher rainfall.

Owing to these similarities, the two gradients amplify each other with respect to temperature, humidity and evapotranspiration. As the coast-inland gradient is much steeper than the temperate-tropical gradient, the dominating ecological gradient of the Namib Desert runs in a WSW-ENE direction. In general, the ecology, flora and vegetation are most conveniently interpreted as a coast-inland zonation with certain variations due to geomorphological, edaphic or historical features.

9.2.1 Coast-inland gradients

The sharp contrast between the coast with its high humidity and mild temperatures and the hot and often extremely dry hinterland has already been described in earlier publications (e.g. Walter 1986). Recently, more detailed information on the steepness and shape of this gradient has contributed additional insights.

Many parameters do not increase or decrease uniformly along the gradient. This is true for temperature, with maxima at the foot of the Great Escarpment, but milder temperatures near the coast and at higher altitudes on the escarpment (Fig. 9.2). Similarly, there is a zone of minimum humidity located between the humid oceanic air and (in summer) the humidity of the summer-rainfall zone further inland.

The position of the zone of lowest humidity varies almost hourly. In the late morning, humidity can be evenly distributed across the gradient or, as a result of hot east or 'bergwinds', be lowest close to the coast. During the day the sea breeze penetrates progressively further inland and in early afternoon this zone of lowest humidity can move some 50 or 100 km inland. The additive effect of the temperature and humidity curve results in conditions least favourable for plant growth being located somewhere between the coast and the escarpment.

The gradients show extreme steepness along the first 20 km near the coast, but become more gentle further inland (Fig. 9.3).

The coast-inland gradients show latitudinal variations; they are steeper in the north and shallower in the south. This latitudinal pattern is caused mainly by the larger extension of the winter-rainfall zone in the south and by the more extreme differences between the cool and foggy Benguela coast and the hot hinterland in the northern subtropical region. The maximum of aridity is close to the escarpment in the south, because of the strong influence of the winter rainfall along the coast which reaches relatively far inland. In the north the maximum aridity is closer to the sea, because the influence of the summer rainfall is stronger and reaches further westwards.

The highest incidence of fog is along the coast (Fig. 9.1*a*), particularly in the central Namib area between Cape Cross (north of Swakopmund) and Walvis Bay, where >100 fog days were recorded during 1984 (Olivier 1995). Fog day frequency decreases northwards and southwards along the coast from this zone; fog penetrates further inland most frequently in this central Namib zone. There are considerable seasonal variations in the frequency of fog. This shows a peak in the winter months at Swakopmund, Alexander Bay and Vredendal, but is highest in summer at Gobabeb and Port Nolloth (but see Olivier 1995). This indicates several types of fog, each possessing different dynamics.

Three types of fog have been reported hitherto, and a fourth is added here. Besides the normal sea fog, driven inland by slow air movements at low altitude, ground fog layers can be produced by condensation after rapid cooling of the soil surface at night. A third type of fog involves the seaward flow of cold air, which mixes with humid and warmer coastal air (K. Loris, pers. comm.). In addition to these three, there are also low cloud layers, which are driven inland by air movements. Near the coast these can be observed as stratified cloud layers, but they touch the ground at 30 to 80 km inland of the coast, e.g. at Gobabeb or east of the Rössingberge, resulting in fog precipitation without salt content. This fog is similar to the 'Garua fog' in the Lomas in Peru and Chile (Walter & Breckle 1984). The seasonality pattern of Gobabeb (Fig. 9.1*a*) suggests that this fog is strongest in summer. Further investigation of the spatial and temporal variation of these fog types is urgently needed.

9.2.2 Geomorphological and edaphic features

The most important latitudinal variation in geomorphology and soils is due to the existence of vast dunefields, especially in the region of the southern Namib sand sea between Lüderitz and Walvis Bay, and to a lesser degree in the Sperrgebiet (Diamond Area) south of Lüderitz and

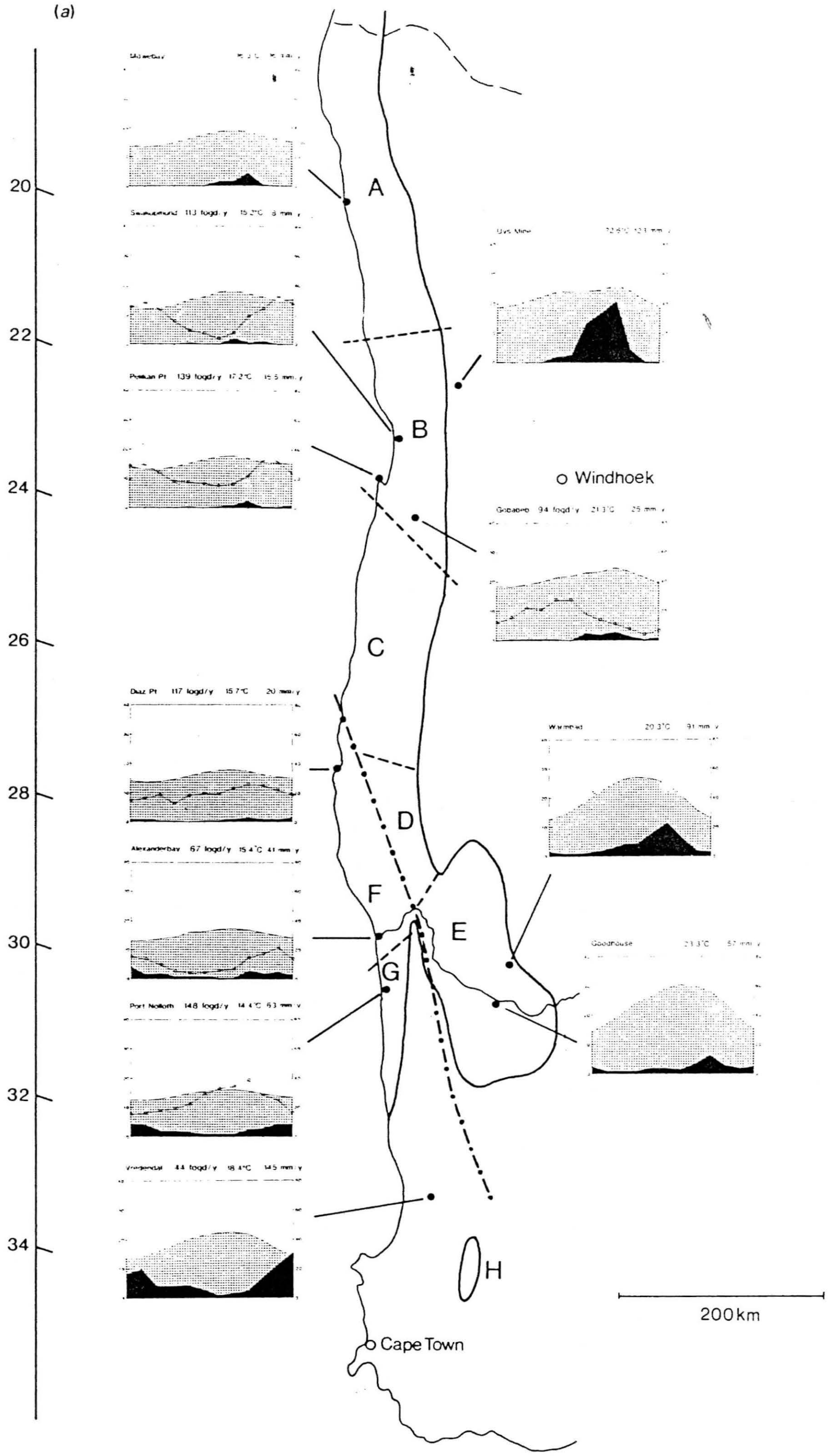
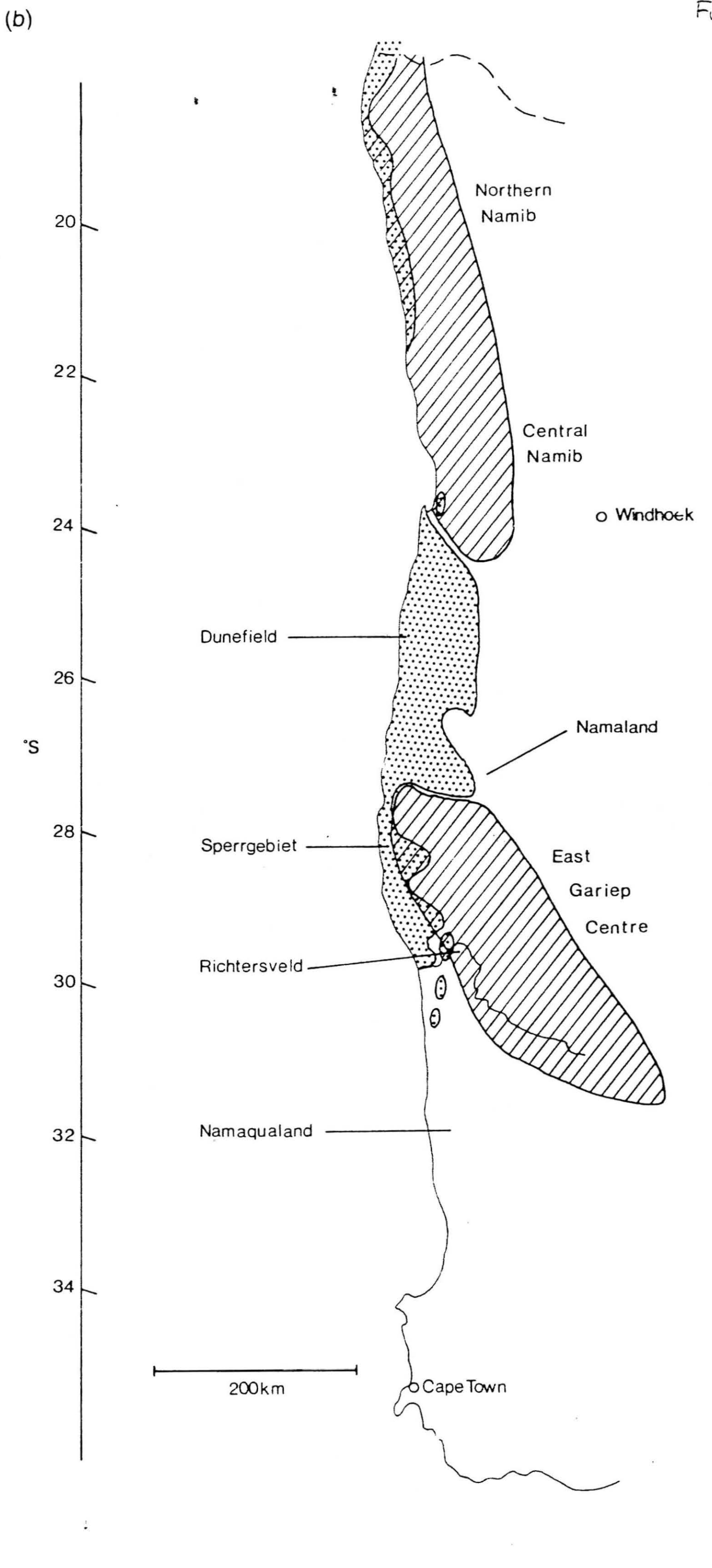


Figure 9.1(*a*). **Arid regions below 100 mm mean annual precipitation (solid black line) with subdivisions of the Namib Desert and selected Walter-Lieth climate diagrams (*x*-axis = July to December; black shading, mean monthly precipitation; grey shading, mean monthly temperature; in some of the diagrams an additional line shows mean number of fog days month^{-1}) and the eastern limit of the winter-rainfall climate (dotted line): A, Northern Namib; B, Central Namib plains; C, Central Namib dunefield; D, Southern Namib (Nama-karoo part); E, East-Gariep Namib; F, Southern Namib (succulent karoo part); G, Northwestern Namaqualand Sandveld; H, Ceres Karoo. (*b*) Dunefields of the Namib Desert (dotted). Two phytogeographical subdivisions (hatched) inside the region with less than 100 mm mean annual precipitation are separated by the large Central Namib dunefield: East Gariep Centre in the south, Central and Northern Namib Centre in the north.**

This part belongs to Figure 9.1(b) on p. 192; please include it there!

Figure 9.1b


(b)
Northern
Namib
20
22
Central
Namib
o Windhoek
24
Dunefield
26
Namaland
°S
28
Sperrgebiet
East
Gariep
Centre
Richtersveld
30
32
Namaqualand
34
200km
Cape Town

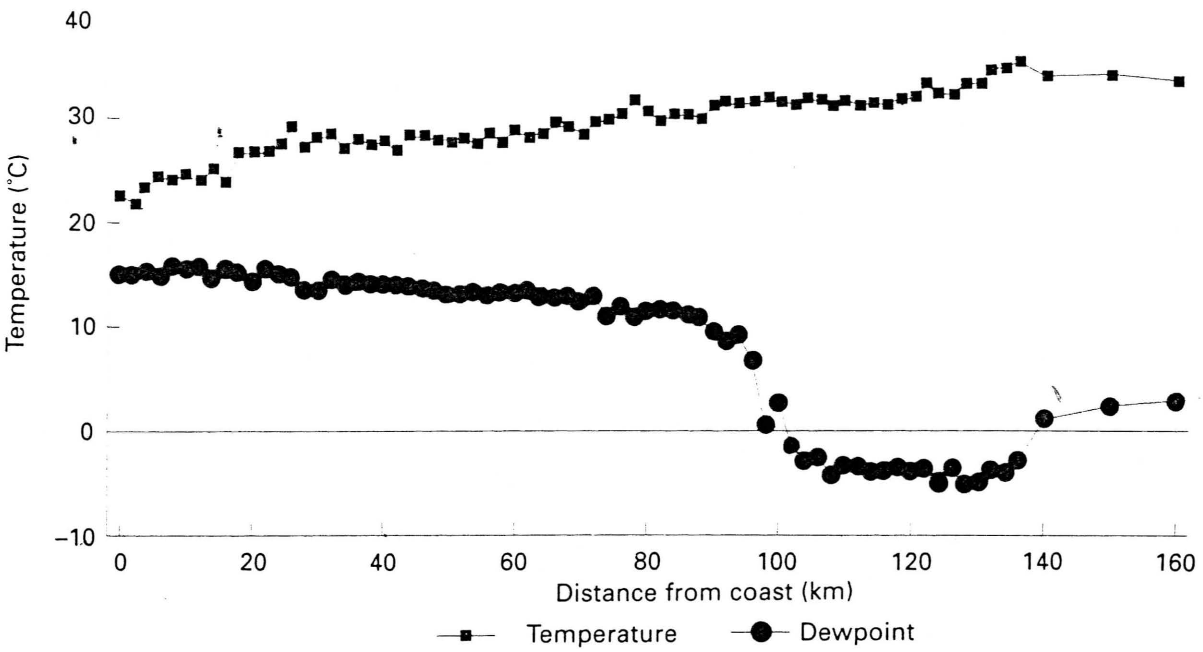


Figure 9.2. **Coast–inland transect (Swakopmund to Karibib) measurement of air temperature and humidity (dewpoint) around midday, showing the extension of moist oceanic air masses (sea breezes) to nearly 100 km inland and the position of the minimum in humidity lying between the eastern limit of oceanic air (c. 100 km) and the western limit of moist air originating from summer rains further inland (140 km).**

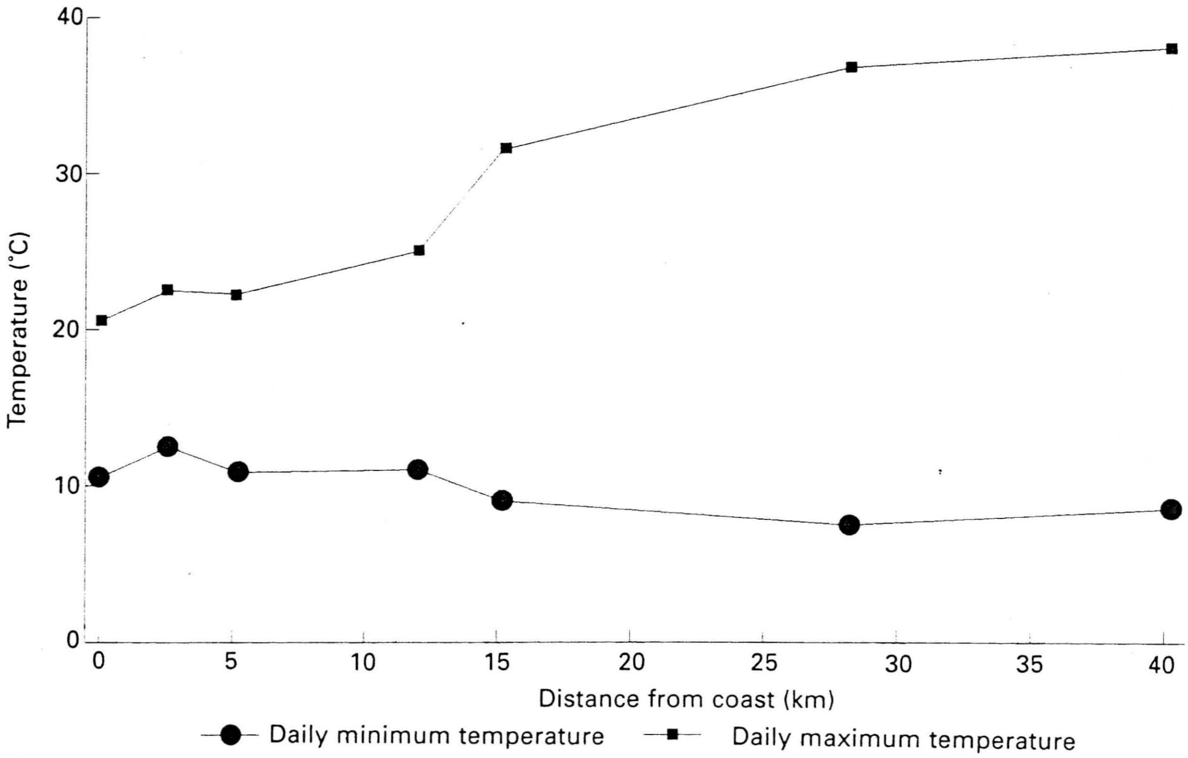


Figure 9.3. **Measurement of daily maximum and minimum temperature along a transect running inland from Lüderitz (S. Fanroth, unpubl. data). Gradients are steep close to the coast and shallow further inland.**

along the northern Namib (Fig. 9.1*b*). The southern Namib sand sea, because of its great age of at least 15 million years (Ward & Corbett 1990), is the most important biological discontinuity of the desert.

At a regional level the ecological and floristic differentiation is influenced by edaphic features such as duricrusts of different composition (silcretes, calcretes, gypsum crusts, salt crusts) and soil surfaces of different structure and composition. Some of these soil types, e.g. quartz pebblefields and gypsum crusts, clearly support a distinct flora (N. Jürgens, unpubl. data). The development of some of these edaphic surfaces is controlled by zonally structured climatic parameters. For example, the distribution of gypsum crusts is limited to low-lying areas in the coastal fog zone.

Geological formations are important determinants of vegetation patterns, e.g. the granites in the Richtersveld (N. Jürgens, unpubl. data). Topographical variation is most clearly visible on outcrops in the Namib plains, which receive higher precipitation and support greater plant biomass. A more complex pattern associated with topography is caused by the interruptions of the Great Escarpment, such as in the central Namib and in the Richtersveld. In the vicinity of the lower Orange River, the lack of the Great Escarpment influences the regional climate considerably, as a strong exchange of air masses takes place between the cool coastal region and the extremely hot inland basin between the eastern Richtersveld and the southern Kalahari.

9.3 Boundaries and patterns

9.3.1 Biome-scale

The desert biome is adjacent to the Nama-karoo and succulent karoo biomes and can best be understood as the extremely arid region of these two biomes. Climatically, the arid conditions are mainly a result of dry and descending air associated with the subtropical high-pressure zone. Because of the involvement of air masses belonging to different circulation cells (circumpolar fronts and tradewind cells), subtropical deserts generally can be divided into two different parts, a more temperate one and a more tropical one. The Namib is the zone between these two rain-transporting systems and consequently has very low precipitation.

These basic climatic patterns define the two different subdivisions of the Namib Desert, a tropical northeastern and a temperate southwestern subdivision, both supporting their own flora. In the tropical subdivision the flora is part of the Nama-karoo phytogeographical region of the Palaeotropics, while the temperate subdivision is occupied by the flora of the succulent karoo phytogeographical region of the Greater Cape Flora (Jürgens 1991, see also Chap. 3, this volume). This subdivision is maintained throughout this chapter.

There is, in fact, a climatic continuum, ranging from 'succulent karoo proper' through 'succulent-karoo desert' to 'Nama-karoo desert' and finally 'Nama-karoo proper'. Owing to this, a wide range of definitions for the Namib Desert have been used in the literature. Researchers in the central and northern Namib define desert as the region that experiences mean annual precipitation below 100 mm and is bounded in the east by the 1000-m contour along the escarpment (Seely 1987). Essentially, this defines the Namib as a coastal desert. Other authors stress the notion of a coastal fog desert and include the foggy coastal regions of Namaqualand (Koch 1962; Von Willert *et al.* 1992). The definition of the desert biome, based on the predominance of therophytes (Rutherford & Westfall 1986), is problematic, because of the high temporal variability of deserts and hence, the episodic occurrence of this life form.

Furthermore, because of the strong climatic differences between the Nama-karoo and succulent karoo portion of the desert, no definition for the desert biome can be proposed that allows an entirely satisfactory delimitation of the biome from both neighbouring biomes (cf. Evenari 1985). Along its eastern border the desert biome is replaced by the Nama-karoo biome, because of higher summer rainfall, whereas the combined effect of lower temperatures, high humidity and rainfall separates the succulent karoo biome from desert in the southwest.

Areas desertified by human-induced degradation can often not be distinguished from natural deserts: this causes additional confusion when a separation of desert and the neighbouring biomes is attempted. Therefore, the use of phytochorological patterns as an additional and perhaps more reliable basis for a delimitation of the Namib Desert seems appropriate. Phytochorological patterns in both the Nama-karoo biome and the succulent karoo biome support the use of the 100-mm isohyet as a first approximation of the boundary of the desert biome (Jürgens 1991). However, if one defines the desert biome as having less than 10% cover of perennial vegetation (Shmida 1985), then one would need to use the 60-mm isohyet to separate desert from succulent karoo, as this would match the same vegetation cover as along the 100-mm isohyet in the Nama-karoo. If the phytogeographical patterns of Namib Desert species are compared with the boundaries as proposed by the biome concept (Rutherford & Westfall 1986; see also Chap. 5, this volume), two implications emerge.

Firstly, there is a large extension of the eastern border. The distribution of 107 taxa ~~occurs~~ extends exclusively in the Nama-karoo phytogeographical region (Jürgens 1991) below 100 mm mean annual precipitation (Fig. 9.1*b*). There are clear discontinuities at nearly all margins, although the dunefield of the central Namib divides the Nama-karoo phytogeographical region into two subunits. The inland region between the Richtersveld, Hunsberge and the Pofadder–Upington region has recently been recognized as a part of the Namib, namely the East-Gariep Centre (Jürgens 1991).

Secondly, there is a vague southern border. There is no clear discontinuity between the flora of the winter-rainfall Namib and the succulent-karoo phytogeographical region proper. Nevertheless, the change in composition does not form a continuum but rather a cascade of steps. One of the more important steps confirms a Namib border close to a 60-mm isohyet in the northern Richtersveld, as proposed by Werger (1978). Another more important step close to the 100-mm isohyet includes the coastal lowlands and intermontane plains from the Richtersveld to near Kleinzee. On the other hand there is a large number of species linking the whole strip of the succulent karoo phytogeographical region from the Sperrgebiet to the Knersvlakte, even including the Little Karoo. Considering that large parts of the Ceres Karoo with very sparse vegetation also receive less than 100 mm annual rainfall, the inclusion of these regions into a larger Namib concept is appropriate.

9.3.2 Regional- and landscape-scale

Within the boundaries of the desert biome, regional subunits can be recognized. These have been described as very pronounced centres of endemism (Jürgens 1992).

East-Gariep Centre The most important centre of endemism in the Nama-karoo portion of the Namib lies in the triangle bounded by Lüderitz, Steinkopf and Upington. Here a wide belt of inland landscapes has to be included in the Namib, including the inland areas east of the Hunsberge–Richtersveld mountain ridges (Fig. 9.1*b*).

Central Namib Centre The second important centre in the Nama-karoo portion of the Namib is found in the plains north of the dunefield.

Southern Namib Centre This centre of endemism belongs predominantly to the succulent karoo phytogeographical region and is situated in the triangle between the Richtersveld, Alexander Bay and Lüderitz.

Obviously the major climatic differences, especially seasonality of rainfall, are the major determinants that separate the Southern Namib Centre (winter-rainfall zone) from the two other phytogeographical centres. The separation of the East-Gariep Centre and the Central Namib Centre (interrupted by the great dunefield of the Namib) may be due to historical reasons. These two centres are held together by the occurrence of a large number of species with disjunct distributions and a high number of closely related species, e.g. *Euphorbia gregaria* and *Euphorbia damarana*, which occur north and south of the dunefield, respectively (N. Jürgens, unpubl. data).

9.3.3 Community-scale

The ecological gradients, described in 9.2, are clearly correlated with changes in floristic composition and vegetation structure. The majority of species have an elongated distribution along a NNW–SSE axis and a narrow west–east distribution, owing to the steepness of the coast-inland ecological gradient. The distribution of community types shows a similar pattern.

A community-level analysis of the Namib vegetation raises a number of problems. Firstly, plant cover is often too low for meaningful community delineation. Secondly, the frequent occurrence of monotypic vegetation units, the high importance of local endemism in the southern Namib and the steep ecological gradients result in a considerable number of communities. Thirdly, the high temporal variability, especially of short-lived species, makes it difficult to document the potential vegetation of many desert habitats.

A comprehensive treatment of the plant communities is beyond the scope of this chapter. Therefore, we present a broad description of the vegetation of the most important major habitats of the desert, i.e. plains, mountains, inselbergs, dunes and rivers (Table 9.1). Tables 9.2 and 9.3 provide brief descriptions of broad community types. These types have been delineated by multivariate analysis of 948 relevés (N. Jürgens, unpubl. data).

9.3.3.1 *Plains*

Vast plains comprise most of the surface area of the Namib Desert. Vegetation of the plains represents the zonal vegetation in the sense that water balance is based on the regional climate without additional benefits such as runoff or groundwater in river beds or sand dunes. Composition, structure and functional aspects of the vegetation of the Namib plains have been treated by numerous authors qualitatively (Giess 1981; Walter 1986), and Robinson (1976) and Moisel & Moll (1981) provide quantitative phytosociological treatments of parts of the plains of the central Namib. Vegetation analyses of the plains of the southern Namib and parts of the East-Gariep Namib are based on our unpublished data. The vegetation of the plains shows large differences across the desert. The eastern summer-rainfall parts of the central Namib, characterized by the dominant stem succulent, *Euphorbia damarana*, shares almost no species

Table 9.1. **Major vegetation zones in the desert biome of southern Africa**

Vegetation zone	**Structural characterization**	**Dominant species**	**Mean species richness/ 100 m^2**	Environment
I Coastal Zone (succulent karoo phytogeographical region)	Dwarf open succulent shrubland and lichen fields	*Zygophyllum clavatum, Drosanthemum paxianum, Ramalina capensis, Teloschistes capensis, Cladoraphis cyperoides*	8–11	Very high humidity, fog frequent, mild temperatures
II Temperate Zone of Namib plains (succulent karoo phytogeographical region)	Dwarf open succulent shrubland	*Zygophyllum stapffii, Z. prismatocarpum, Z. cordifolium, Arthraerua leubnitziae, Othonna furcata, Brownanthus schlichtianus, B. arenosus, Stipagrostis sabulicola, S. lutescens*	3–12	High humidity, rel. mild to warm temperatures
III Temperate Namib mountains (succulent karoo phytogeographical region)	Dwarf to low open succulent shrubland	*Eberlanzia* spp., *Tetragonia* spp., *Ruschia* spp., *Sphalmanthus* spp., *Stoeberia* spp., *Pteronia* spp., *Tylecodon paniculatus, Galenia dregeana, Ceraria fruticulosa*	6–12	High humidity, mild temperatures
IV Zone of minimum vegetation	Extremely sparse dwarf to small succulent shrubland	*Salsola tuberculata, Sarcocaulon* spp., *Zygophyllum simplex*	0–3	Mild to high temperatures, low humidity
V Eastern grassland and stem succulent shrubland zone (Nama-karoo phytogeographical region)	Grasslands (on fine textured soils) and tall stem succulent shrubland (on rocky ground)	*Calicorema capitata, Stipagrostis* spp., *Euphorbia gregaria, E. damarana, E. virosa, Acacia reficiens, Aloe dichotoma*	3–7	Warm to very high temperatures, low humidity
VI Transition to Nama-karoo shrubland (Nama-karoo phytogeographical region)	Tall stem succulent shrubland or open savanna	*Rhigozum trichotomum, Parkinsonia africana, Boscia* spp., *Euphorbia guerichiana, Cyphostemma* spp., *Commiphora* spp., *Moringa ovalifolia, Myrothamnus flabellifolius*	5–12	Warm to very high temperatures, low humidity

bold type

italics

Table 9.2. **Major plant communities in the succulent karoo phytogeographical region of the desert biome**

separate

Zone	**Community**	**Other diagnostic species**	**Environment**	**Geography**
I	*Zygophyllum clavatum*	*Brownanthus marlothii, Othonna furcata, Didelta carnosa var. tomentosa*	Coastal dunes, saline fine-grained soils	Coast from Richtersveld to Northern Namib
I	Subcommunity with *Ramalina capensis*	*Limonium dyeri, Hypertelis angrae-pequenae*	Fog dependent, sand storm resistant	Port Nolloth to Lüderitz
I	Subcommunity with *Teloschistes capensis*		Fog dependent, on gypsum soils	Alexander Bay to Northern Namib
I	Subcommunity with *Lebeckia multiflora, Cladoraphis cyperoides*	*Lebeckia cinerea, Othonna cylindrica, Cladoraphis spinosa, Brownanthus arenosus, Lycium cinereum, Eberlanzia sedoides*	Coastal dunes and sandy valleys	Namaqualand to Northern Namib
1	Subcommunity with *Salsola zeyheri, Cephalophyllum ebracteatum*	*Psilocaulon dinteri, Pteronia glabrata, Sarcocaulon patersonii, Drosanthemum paxianum, Tetragonia decumbens, Juttadinteria deserticola*	Coastal, saline and rocky soils	Richtersveld to Lüderitz
I	Subcommunity with *Arthraerua leubnitziae*		Coastal, saline and loamy or sandy soils	Central Namib to Northern Namib
I	Subcommunity with *Dracophilus dealbatus*	*Eberlanzia* sp., *Ruschianthemum gigas*	Stony hills and plains	Lower Orange River
I/II	*Stipagrostis sabulicola*		Coastal to inland dunes	Sperrgebiet to Namib dunefield
II	*Brownanthus schlichtianus*	*Trachyandra muricata, Oncosiphon piluliferum, Senecio cardaminifolius, Aridaria noctiflora, Hypertelis salsoloides, Mesembryanthemum squamulosum*	Silty or loamy soils (often desert loess) over calcrete	Richtersveld to Lüderitz
II	*Zygophyllum prismatocarpum*	*Mesembryanthemum pellitum, Cheiridopsis robusta, Trianthema parvifolia, Euphorbia chersina, Psammophora modesta, P. nissenii*	Eroded calcretes	Richtersveld to Lüderitz

Table 9.2 Cont

Zone	Community	Other diagnostic species	Environment	Geography
II	*Arthraerua leubnitziae*	*Zygophyllum stapffii*	Mainly gypsum crusts	Central Namib
II	*Zygophyllum stapffii*	*Salsola tuberculata, Sesuvium sesuvioides*	Mainly calcretes	Central Namib
II/III	*Brownanthus pubescens*	*Delosperma pergamentaceum, Portulacaria pygmaea*	Shallow soils with gypsum crusts or calcrete and high salinity	Lower Orange River region
III	*Galenia dregeana*	*Ruschia* sp., *Euphorbia chersina, Crassula grisea, Othonna opima*	Neutral to acid loamy soils	Richtersveld and Sperrgebiet
IV	Ephemerals	*Synaptophyllum juttae, Opophytum aquosum, Stipagrostis obtusa, Zygophyllum simplex*, etc.	Plains and valleys	Richtersveld to Northern Namib

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Table 9.3. **Major plant communities in the Nama-karoo phytogeographical region of the desert biome**

Zone	Community	Other diagnostic species	Environment	Geography
V	*Sisyndite spartea*	*Zygophyllum microcarpum, Rogeria longiflora*	Sheetwash plains and rivers	East Gariep Namib
V	*Sphalmanthus tetragonus*		Sandy and loamy plains	East Gariep Namib
V	*Euphorbia gregaria*		Rocky plateaux or crusts	East Gariep Namib
V	*Euphorbia virosa*	*Ceraria namaquensis, Pachypodium namaquanum*	Rocky mountains	East Gariep Namib
V	*Euphorbia damarana*		Rocky plateaux or crusts	Central Namib to Angola
V	*Stipagrostis ciliata (Euphorbia gummifera)*	*Calicorema capitata, Stipagrostis obtusa, S. geminifolia, Eragrostis nindensis*	Sandy plains, mostly with calcrete	East Gariep Namib to Central Namib
V	*Stipagrostis seelyae*		Eastern dunes	Central Namib dunefield
VI	*Rhigozum trichotomum*	*Parkinsonia africana, Boscia foetida*	Silty, loamy to gravelly plains	East Gariep Namib to Namaland
VI	*Commiphora virgata*	*Commiphora tenuipetiolata, C. glaucescens*	Rocky ground	Eastern Central and Northern Namib

with the plains covered by *Brownanthus schlichtianus* and other leaf-succulent chamaephytes in the winter-rainfall part of the Namib.

Lichen Fields Lichen fields form a characteristic constituent of the Namib vegetation near the coast. In the Central Namib, on fine-grained soils, *Teloschistes capensis* is the most important lichen species, whereas on stones and rocks, lichen communities are species-rich (Schieferstein & Loris 1992). High fog precipitation is a necessary prerequisite of the lichen fields, while the sand-blasting effects of strong easterly winds might explain the absence of lichen fields in other fog-rich coastal areas (Schieferstein & Loris 1992). The vast lichen fields of the central Namib have their southern limit near the great dunefield, where the incidence of sand blasting is very high. However, two very well-developed, but isolated, lichen fields occur near Alexander Bay and Lüderitz (Jürgens & Niebel 1991) and at least two more lichen fields exist between Lüderitz and Oranjemund, both situated a few kilometres inland of the coast near Elizabeth Bay and Chameis (G. Williamson, pers. comm.).

Extensive fruticose lichen vegetation on fine soil is limited to sites where environmental conditions are disadvantageous for angiosperms (e.g. high salinity, extremely low rainfall). Generally, taller angiosperms harvest the fog before it touches the ground and therefore epiphytic lichens predominate (Jürgens & Niebel-Lohmann 1995). Lichen fields dominated by *Teloschistes capensis* are limited to soils containing gypsum (Fig. 9.4), but only *Ramalina capensis* is able to withstand frequent sand storms and stabilizes dunefields.

Central and northern Namib The western part of the central Namib, from the coast to some 40 to 60 km inland, is dominated by two low (0.6–0.7 m tall), halophytic nanophanerophytes, namely *Arthraerua leubnitziae* and *Zygophyllum stapffii*. *Arthraerua leubnitziae* occurs frequently in saline habitats in almost any topographic position in the western half of this belt, but further inland it is concentrated along large drainage channels. This species extends about 80 km inland in the southern cen-

Figure 9.4. **Lichen field on eroded gypsum soils at Alexander Bay, South Africa, dominated by *Teloschistes capensis* with occasional *Ramalina capensis* and individuals of *Sarcocaulon* sp. (Geraniaceae) and various Mesembryanthemaceae (Photo: D.M. Richardson).**

Figure 9.5. **Zone of minimum vegetation on the central Namib plains, about 80 km east of Walvis Bay, Namibia. Plant life comprises a few individuals of the annual form of *Stipagrostis ciliata* (Photo: R.M. Cowling).**

Figure 9.6. ***Acacia erioloba* on the eastern fringes of the central Namib (Photo: R.M. Cowling).**

tral Namib. *Zygophyllum stapffii* is commonly found in this temperate coastal zone, but, in most regions, reaches 10 to 20 km further inland than *A. leubnitziae*, often following drainage lines with deeper soils. Both species occur on the coast and are clearly tolerant of high soil salinity. The habitat spectrum of *Z. stapffii* is wider than that of *A. leubnitziae* and includes rocky outcrops (Robinson 1976). Both species may be accompanied by *Salsola tuberculata* over their entire distribution ranges. These species exist at the extreme end of the spectrum of alkalinity and salinity in the zonal habitats of the central Namib (N. Jürgens, unpubl. data).

Inland of the *Zygophyllum–Arthraerua* belt, there is a zone of extreme aridity almost devoid of vegetation (Besler 1972; Fig. 9.5). Shallow rocky soils are more favourable sites, supporting a sparse vegetation, whereas homogeneous fine-grained soils in this zone are often totally devoid of perennial plant life. Common species include *Salsola tuberculata*, which also occurs in the coastal region and further inland. Phreatophytes such as *Welwitschia mirabilis* or *Acacia reficiens* may represent the only perennial plants along the shallow drainage lines. However, these species are more frequent further inland and are more appropriately described as extrazonal outliers of the transition zone to the Nama-karoo biome. // As the amount and frequency of summer rainfall increases east of the zone of minimum vegetation, there is an increase in the vegetation cover and species richness (Cowling *et al.* 1994). Many species in this region are drainage-line specialists and never or rarely occupy zonal habitats of the plains. Examples are *Petalidium setosum* (Günster 1993c), *Pechuel-Loeschea leubnitziae*, *Asclepias buchenaviana* and *Adenolobus pechuelii*. Many other species, e.g. Calicorema capitata, are concentrated along drainage lines in the most arid parts of the Namib, but form diffuse vegetation on the plains further eastward, owing to increasing summer rainfall.

no gap

italic

Another unit east of the zone of minimum vegetation is dominated by the stem-succulent *Euphorbia gregaria*. These tall plants (up to 3 m high) are associated with a number of other taxa belonging to the Nama-karoo phytogeographical region such as *Boscia foetida*, *Calicorema capitata*, *Acacia reficiens* and *Maerua schinzii*. On sandy soils, this community is replaced by grasslands with an admixture of *Kissenia capensis*, *Petalidium* spp. and *Geigeria* spp. Dominant grasses that form dense swards on sandy soils, and also on the calcrete plains at the eastern margin of the Namib, are *Eragrostis nindensis* and *Stipagrostis ciliata*. These areas are dissected by drainage channels which, depending on their size, depth and water storage, support the above-mentioned chamaephytes or tall trees such as *Acacia erioloba* (Fig. 9.6).

The absence or extreme rarity of young plants of *Wel-*

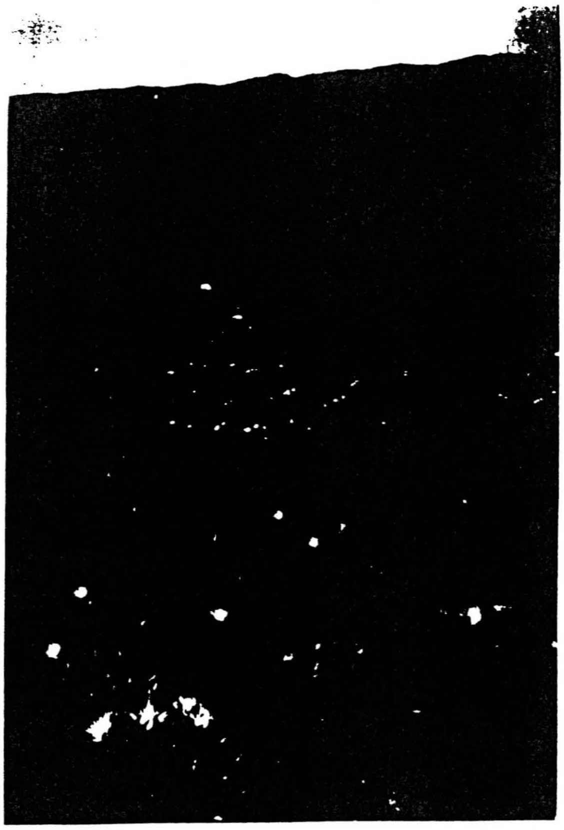


Figure 9.7. **Succulent vegetation dominated by *Cheiridopsis robusta* (Mesembyranthemaceae) in the southern Namib near Alexander Bay (Photo: P.G. Desmet).**

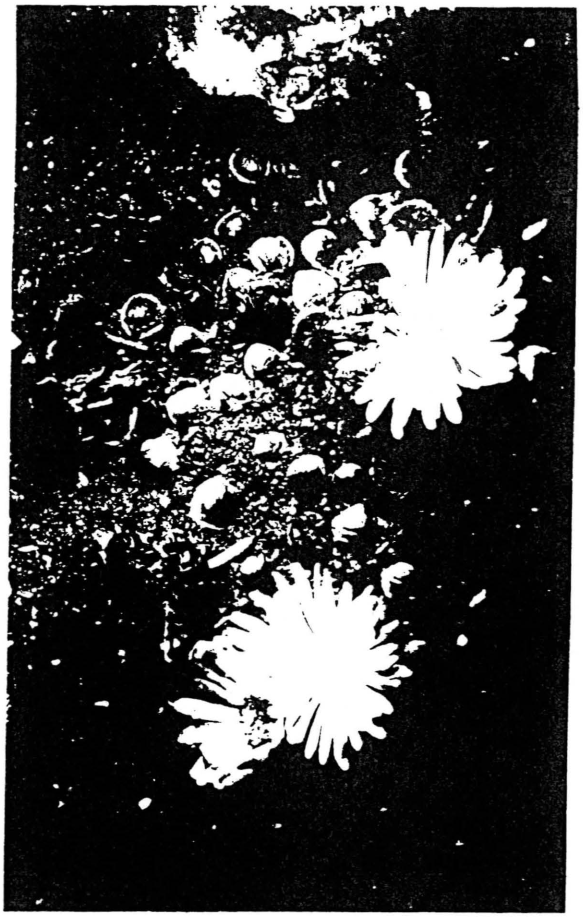


Figure 9.8. ***Fenestraria rhopalophylla* ssp. *aurantiaca* (Mesembryanthemaceae), a 'window plant' endemic to the foggy southern Namib (Photo: P.G. Desmet).**

witschia mirabilis in the coastal zone and in the zone of minimum vegetation is puzzling in view of the ability of adult plants of this long-lived species to cope with these habitats. In the case of *W. mirabilis*, only populations in the sparse savannas of Damaraland, Kaokoland and southwestern Angola show a normal demographic structure. This suggests that old plants may have persisted in desert conditions after recruiting in savanna-like environments many thousands of years ago (Jürgens 1992). Interestingly, the transpiration rate of 1 l m^{-2} leaf surface day^{-1} (Von Willert *et al.* 1982) is high compared to other evergreen plants of the Namib (Von Willert *et al.* 1992).

Southern Namib The plains of the southern Namib are covered by species of the succulent karoo phytogeographical region (Jürgens 1991; Fig. 9.7) which is best described as a more sparse extension of the vegetation of northwestern Namaqualand, especially the Richtersveld and the lower Orange River valley. However, many species are endemic to the region between about 26 and 28° S.

Fog incidence as a measure of distance from the cool foggy coast is a major determinant of community structure (Fig. 9.8). A very important factor is the impact of storms, which are of extraordinary force and frequency in the coastal part of the southern Namib. These winds are ecologically extremely important, because of their sand-blasting effect.

Along the coast, *Zygophyllum clavatum*, *Brownanthus marlothii*, *Didelta carnosa*, *Drosanthemum paxianum* and *Tetragonia decumbens* comprise a community that can be subdivided into several subunits. The immediate coastal zone, where fog incidence is highest, supports numerous lichen species, including *Ramalina capensis*, and a high frequency of the angiosperms *Limonium dyeri* and *Hypertelis angrae-pequenae*. Further inland on sandy soils in warm sheltered valleys, this community is replaced by one dominated by *Lebeckia multiflora*, *Eberlanzia sedoides*, *Lycium cinereum*, *Othonna arbuscula* and *Helichrysum obtusum*.

A community, almost exclusively composed of perennial species including *Salsola zeyheri*, *Cephalophyllum ebracteatum*, *Juttadinteria deserticola*, *Sarcocaulon patersonii*, *Pteronia glabrata* and *Euphorbia verruculosa*, is found on very shallow soils on rocky ground from the coast to some 20 km inland. In the Lüderitz region, east of the coastal zone, very little vegetation occurs on the wide plains to the east with mass germination of annual grasses and succulents following good rains.

South of Grillental and inland of the abovementioned units, the plains are covered by several species-rich communities. On silty loamy soils on calcrete, *Brownanthus schlichtianus*, *Aridaria noctiflora*, *Mesembryanthemum squamulosum*, *Foveolina albida*, and *Hypertelis salsoloides* form a distinctive unit that can include more than 10 species 100 m^{-2}. Dolomite rock is typically occupied by a community with *Euphorbia chersina*, *Zygophyllum prismatocarpum*, *Psammophora modesta*, and *P. nissenii*, whereas eroded calcretes often support a community dominated by *Z. prismatocarpum*.

A community characterized by the tall stem-succulent *Euphorbia gummifera* covers large areas of calcrete. These areas are sometimes covered by sands, in which case grasses such as *Stipagrostis obtusa* and *S. geminifolia* commonly occur, as well as *Brownanthus arenosus*. *Augea capensis* is frequently found on more saline plains.

The northeastern part of the southern Namib is covered by species of the Nama-karoo phytogeographical region (Jürgens 1991). In the hot valleys of the Hunsberge and the northern Richtersveld (succulent karoo phytogeographical region), fine-grained soils support communities with *Rhigozum trichotomum* and *Parkinsonia africana* (both Nama-karoo species). Similarly, rocky ground is covered by vast *Euphorbia gregaria* stands, and sometimes *Aloe dichotoma* and *Kissenia capensis* are found. Grasses such as *Stipagrostis geminifolia*, *S. ciliata* and *S. obtusa* are found on sandy soils. Aspects similar to the eastern margin of the central Namib are found, where drainage channels form tree lines with *Acacia erioloba*.

Inland of the Hunsberge, from Namaland to the Upington region, vast rocky plains are covered by stands of *Euphorbia gregaria*. In the East-Gariep Namib east of the Hunsberge and the Richtersveld, sheetwash valleys form an important part of the landscape, and support vegetation similar to that of river beds. A characteristic species is *Sisyndite spartea* (Fig. 9.9).

9.3.3.2 *Mountains*

True montane deserts occur in the high elevation areas of the Diamond Area, especially the Hunsberge and the Richtersveld. This mountainous area supports an exceptionally rich flora, clustered in numerous species-rich communities. These communities include species of both the karoo and the Nama-karoo floras.

Composition and community structure are influenced by altitude, topography, geology and aspect. Aspect can be very important: moist air and fog from the coast enter the mountains along regular routes, bringing additional moisture to certain slopes. Nocturnal dew-fall evaporates in the morning more rapidly on northeastern slopes than on southwestern slopes. This also strongly influences vegetation patterns.

Owing to the cooler and more humid conditions, mountains can house enclaves of succulent karoo flora in a Nama-karoo matrix. e.g. Tsaukheib, Hunsberge around Witpüts (Jürgens 1991). Close to the central mountain ridge of the Richtersveld and the Hunsberge, many mountains and valleys show a rapid transition from vegetation of succulent karoo affinity on southwestern slopes to taxa of Nama-karoo affinity on northeastern slopes.

9.3.3.3 *Inselbergs*

In deserts, the vegetation on inselbergs is often more diverse than in the surrounding plains and comprises taxa that usually occur in areas of higher rainfall (Le Houerou 1986; Monod 1986). This is also the case with inselberg vegetation in the Namib. Taxa such as *Xerophyta viscosa*, *Aloe dichotoma* and *Commiphora* spp., which are normally associated with the transitional savanna zone of the escarpment, commonly occur on inselbergs in the desert zone (Giess 1971). In a study in the southern Namib, A. Günster (unpubl. data) found 84 species on an inselberg and fewer than ten species in the surrounding sand sea. Similar figures can be obtained for the central Namib, where inselbergs are surrounded by gravel plains.

The composition of inselberg floras is largely dependent on their geographical position. In the southern Namib, they harbour mainly winter-rainfall taxa such as a variety of Mesembryanthemaceae (*Conophytum saxetanum*, *C. gratum*, *Namibia pomonae*) and Crassulaceae (*Crassula sladenii*). Similarly, inselberg vegetation in the central and northern Namib comprises mainly summer-rainfall taxa such as *Sterculia africana*, *Euphorbia virosa* and numerous *Commiphora* spp. Coastal inselbergs often harbour a variety of lichens as well as dwarf and low succulents such as species of *Lithops*, *Lycium*, *Othonna* and *Pelargonium*, whereas inselbergs further inland are dominated by larger shrubs and trees (*Aloe dichotoma*, *Sterculia africana* and *Commiphora* spp.). The life-form spectra differ accordingly. Leaf-succulents dominate in the south and along the coast (Jürgens 1986), whereas evergreen and deciduous shrubs as well as stem-succulents dominate on inselbergs in the central and northern Namib (Figs. 9.10 and 9.11).

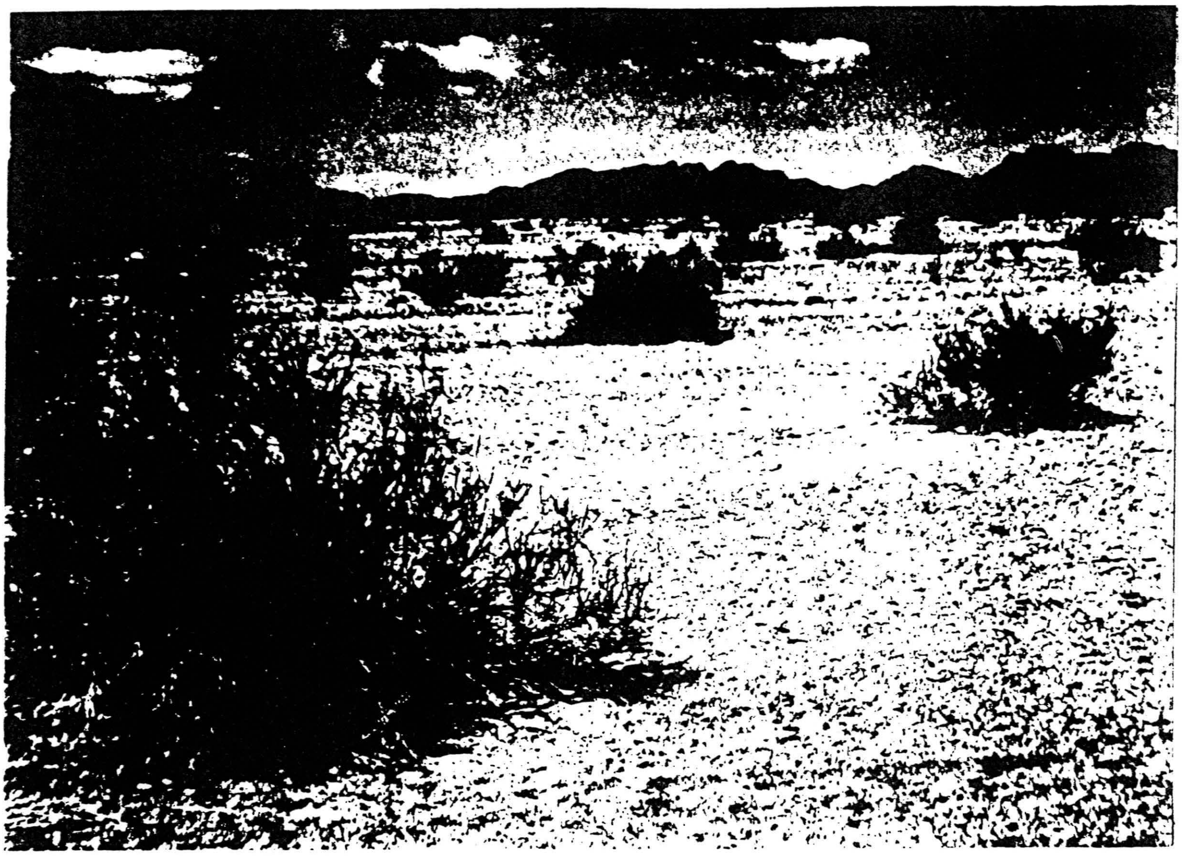


Figure 9.9. ***Sisyndite spartea*** **(Zygophyllaceae), a stem-photosynthetic shrub, forms monospecific stands in the sheetwash plains of the East-Gariep Namib (Photo: N. Jürgens).**

Figure 9.10. ***Euphorbia virosa*** **(foreground) and** ***Maerua schinzii*** **on an inselberg west of the Hartmannberge in the Kaokoland region of the northern Namib (Photo: R.M. Cowling).**

Figure 9.11. **The lower slopes of the Brandberg, a massive inselberg on the fringes of the central Namib that reaches an elevation of 2574 m, supports a diverse tree flora. Shown here is** ***Boscia albitrunca*** **(foreground),** ***Commiphora*** **sp. and** ***Acacia montis-usti*** **(Photo: R.M. Cowling).**

9.3.3.4 *Dunes*

The active Namib dune sea is not devoid of vegetation, despite statements to this effect in the earlier literature (Giess 1962; Walter 1971, 1986; Leistner 1979). Numerous authors have recently described various aspects of the composition and functioning of the central Namib dune sea vegetation (Robinson 1976; Seely & Louw 1980; Yeaton 1988, 1990; Boyer 1989; Seely 1990, 1991; Jacobson 1992). Species diversity in the dunes is low relative to that of other habitats of the Namib. For example, Robinson (1976) recorded 20 species from the central Namib dune sea and 250 from the nearby gravel plains. Of the ten plant species found most commonly in the central Namib dunes, seven are endemic (Robinson & Seely 1980). Generally, the level of endemism in the Namib dunes is exceptional relative to similar areas elsewhere in the world (Bowers 1982; Walter & Box 1983).

The dominant plants of the central Namib dunes are perennial grasses of the genera *Cladoraphis*, *Centropodium* and *Stipagrostis* (De Winter 1990). Succulents are generally uncommon, but the woody-stemmed leaf-succulent *Trianthema hereroensis* (Aizoaceae) is co-dominant with *Stipagrostis sabulicola* in the coastal part of the main dunefield (Seely 1991; Fig. 9.12). *Acanthosicyos horridus* (Cucurbitaceae) occurs from the coast to about 80 km inland, in sandy interdune valleys from near Port Nolloth to at least the Curoca River in southwestern Angola (M.K. Seely, pers. obs.). Annual grasses and herbs form the dominant component on the lower dune slopes and inter-dune valleys, following average rain events. Perennial plants always dominate the upper slopes and, even after unusually high rains, germinants of perennial species are more frequent here (Seely 1990, 1991).

The favourable water relations of the deep dune sands facilitate the development of perennial grassland communities that are not found on the adjacent gravel plains, despite similar rainfall regimes. Grass community structure and richness vary across the dunefield in response to the rainfall gradient and concomitant levels of sand stability (Yeaton 1988).

In the eastern half of the dunefield where rainfall is higher, dune slopes support distinct vegetation zones.

Figure 9.12. **The vegetation of the central Namib dunes is dominated by species of *Stipagrostis* (*S. sabulicola* in the foreground) and other Poaceae (Photo: N. Jürgens).**

Perennial plant species richness and cover are highest on the dune base and plinth zones; lowest richness and cover are on the dune crest and inter-dune plains (Boyer 1989), but annual cover on the inter-dune plains is highly variable from year to year, depending on the amount of rainfall (Seely & Louw 1980; K.M. Jacobson, pers. obs.). Vegetation zonation on the dunes has been attributed to differential tolerance of plant species to the abiotic stresses imposed by the desert climate, namely, moisture availability and sand stability (Yeaton 1988, 1990; Seely 1990, 1991) as well as inter- and intra-species competition (Yeaton 1990).

9.3.3.5 *Rivers*

The 12 major ephemeral rivers crossing the Namib bring additional moisture to the desert. Variation in hydrology and hence composition of the woodlands among riverine systems is largely a function of catchment size and rainfall regimes within the catchments. Small catchments with irregular flows, e.g. the Tsondab and the Tsauchab Rivers, support woodlands composed primarily of *Acacia erioloba*, *A. tortilis* and *Parkinsonia africana*. Larger systems, with regular annual flow, support larger and more tree species. In the central Namib, ephemeral rivers such as the Kuiseb and Swakop support woodlands dominated by *Acacia erioloba*, *Faidherbia albida*, *Ficus cordata*, *F. sycomorus*, *Euclea pseudebenus*, *Salvadora persica* and *Tamarix usneoides*. In addition to these species, the Omaruru and other northern Namibian rivers support *Combretum imberbe* and *Colophospermum mopane*. Species richness of the riparian forests is generally low, but increases from south to north. Forest composition and plant cover varies along the length of the rivers: for example, *Ficus* sp., *Faidherbia albida* and *Tamarix usneoides* occur in more mesic habitats than *Acacia erioloba* and *Euclea pseudebenus* (Seely *et al.* 1980; K.E.A. Leggett unpubl. data; Fig. 9.13). Some river mouths form meandering deltas supporting saline or freshwater marsh vegetation; however, the form of the river mouths varies greatly depending on their annual flood volume.

9.3.3.6 *Special features, occurring in several community types*

Fairy rings A curious phenomenon in the eastern Namib, from Angola to Namaqualand, are circular patches, devoid of vegetation, often referred to as fairy rings (Fig. 9.14). Several hypotheses have been proposed to explain their origin. One proposal is that fungi and/or allelopathic plants (e.g. *Euphorbia* spp.) may exude toxins and thus make the soil unsuitable for establishment of seedlings (Eicker, Theron & Grobbelaar 1982; R.I. Yeaton, pers. comm.). In addition, the decomposition of dead euphorbias, which are abundant in many parts of the eastern Namib, may be responsible for the release of toxins into the soil (Brückner 1977). Another hypothesis invokes the activities of ants and termites (Moll 1994). However, these hypotheses remain to be tested. There are some similarities to the *heuweltjies* (mima-like mounds) found in the succulent karoo biome (Chap. 7, this volume). Both fairy rings and *heuweltjies* are circular in form, and show a regular distribution pattern with 'rings' of different ages in close proximity. However, while *heuweltjies* form mounds, fairy rings form slight depressions. Furthermore, *heuweltjies* often have a biogeneous calcrete formation, whereas fairy rings are associated with gaps in the calcrete crust (Cox 1987). The southernmost fairy rings occur on a plain in the northern Richtersveld, some tens of metres from a *heuweltjie* at the base of a slope (N. Jürgens, pers. obs.).

Figure 9.13. **The Kuiseb River forms the boundary between the Namib sand sea to the south and the gravel plains of the central Namib (foreground). The riverine vegetation, shown here near Gobabeb, is a woodland dominated by *Acacia erioloba* and *Faidherbia albida* (Photo: R.M. Cowling).**

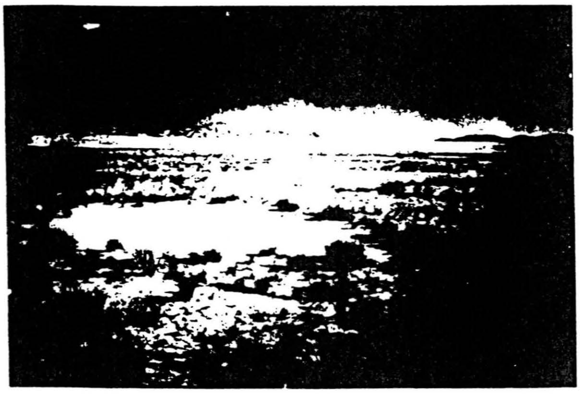


Figure 9.14. **Fairy rings in the sandy plains near Sesfontein in the northern Namib (Photo: R.M. Cowling).**

Microphytic crusts Other important components of desert vegetation are microphytic crusts, consisting of bluegreen and green algae and sometimes bryophytes and lichens (West 1990; Danin 1991; Lange *et al.* 1992). These crusts contribute to nutrient turnover and the redistribution of surface runoff (Gillis 1992). Although microphytic crusts have been observed in the Namib at various locations, nothing is known about their distribution, composition or role in Namib Desert ecosystems. In the coastal fog belt, where gypsum crusts predominate and there is a low but frequent moisture supply, microphytic crusts play an important role. Crusts of lichens (*Heppia* spp.) may be important for silty, loamy and sandy soils in resisting erosion. Similarly, the 'window algae', located several centimetres below the soil surface level and receiving light through quartz stones (Vogel 1955), contribute to biomass production in the Namib Desert.

9.4 Plant types

Very little autecological research has been undertaken on the Namib flora. Therefore, it is not possible to provide an extensive review on the characteristics of all the different plant types in the biome. Rather we highlight a few interesting features in this section.

9.4.1 Annuals and ephemerals

Ephemerals and annuals comprise by far the largest proportion of species in most desert regions (Inouye 1991). Annuals are seasonal and germinate only when rain falls at a specific time of the year, whereas ephemerals germinate whenever there is sufficient moisture, irrespective of season (Von Willert *et al.* 1990). Both plant types have very short life spans, some as short as a few weeks, and may produce seeds within weeks after establishment. Since conditions after sufficient rainfall are almost mesic and ephemerals complete their life cycle before arid conditions prevail again, adaptations to prevent water loss are usually not well developed. Nevertheless, there is a remarkable number of succulent annuals in the temperate part of the Namib Desert, e.g. *Mesembryanthemum* spp., *Opophytum* spp., *Zygophyllum simplex* and *Crassula dichotoma*.

broken letter? Zygophyllum simplex

The ephemeral and annual flora in the Namib differs greatly between regions, mainly due to the differences in prevailing form and pattern of moisture supply. Annual plants add to the species spectrum in nearly all different habitat types, but some habitats such as the zone of minimum vegetation harbour only annual or ephemeral species, e.g. *Stipagrostis* spp. on the gravel plains of the central Namib (Nel 1983; see also 9.3.3.1).

9.4.2 Facultative perennials

To cope with the unpredictability and variability of the Namib Desert environment, many desert plants show a high plasticity in life history parameters, such as life span, growth and reproductive output (Günster 1994a). An example is the large number of species that can either be annual or perennial, depending on the prevailing moisture conditions. They usually grow in drainage lines where plants have access to underground water stores and die when this water source is exhausted, usually after two to several years. The facultative perennials in the Namib flower and produce seeds continuously. Common examples are *Codon royenii* (Günster 1995a), *Rogeria longiflora* and *Kissenia capensis*.

Many species of *Stipagrostis* respond opportunistically, in terms of vegetative growth and reproductive output, to variable precipitation (Walter 1986; Seely 1990). For example, 12 mm of rainfall is sufficient for *S. ciliata* to set seed in a sandy substratum. However, with 25 mm the same plants can build up sufficient reserves to set seed during the first season and then sprout again in response to rains during a second season (Jacobson 1992). Walter (1986) describes the morphology of the root and shoot structure of *Stipagrostis* which enables survival in the dry period. These facultative perennial *Stipagrostis* spp. can grow into large bunchgrasses which, once established, have many advantages over individuals newly established from seed; namely, well-developed root systems and associated mycorrhizae for water and nutrient acquisition (Jacobson 1992, 1995); more rapid development of photosynthetic material in response to rainfall; and more economic use of moisture for growth and seed set (P. Jacobson, pers. obs.).

9.4.3 Geophytes

As in other desert regions, geophytes are a common sight after rains in the Namib. In the succulent karoo portion of the Namib they are more prominent in species number and cover than in the Nama-karoo (Chap.7, this volume). After favourable rains some species (e.g. *Ornithogalum stapffii*, *Dipcadi longifolium* and *Trachyandra laxa*) form extensive stands of one or two species on plains in the central and southern Namib. Apart from casual observations (e.g. Olivier 1984), there are no data on geophyte life cycles and species interactions in the Namib.

9.4.4 Phreatophytes

Phreatophytes, species that are specialized in the exploitation of groundwater, are a common feature of the Namib Desert. A good example is *Acanthosicyos horridus* (Cucurbitaceae), the !nara plant, which is endemic to the Namib dunefields. It is a leafless evergreen (stem photosynthetic) and is active all year round. Its long taproot always reaches water stores deep in the ground, sometimes down to 15 m below the surface.

Welwitschia mirabilis is the most studied plant in the central Namib. However, many unanswered questions still puzzle botanists today. Many consider it to be a tree with its stem half-buried. From the top of the cone-shaped stem, two large leaves grow continually, dying off at the leaf tips. Thus, leaves may reach more than 10 m in length (Bornman 1977). Some individuals are considered to be more than 1000 years old. Recent ^{14}C dating of a small plant of 180 × 550 mm stem diameter indicated an age of 550 years (N. Jürgens, unpubl. data).

A number of physiological studies on *Welwitschia mirabilis* have been concerned with its photosynthetic pathway and its ability to take up fog precipitation. It is now established that *W. mirabilis* is not a primitive CAM plant, as was previously assumed (Bornman 1977), but possesses an ordinary C_3 pathway (Eller *et al.* 1983). It is able to take up fog water, which condenses on the leaf surface and is channelled to the base of the stem, but its ability to take up water through stomata as demonstrated by Bornman (1977) has not been confirmed by Von Willert (1985). Comparisons of water relations, CO_2 exchange, water-use efficiency and growth of *W. mirabilis* plants in three contrasting habitats, including the *Welwitschia* plain approximately 45 km east of the coast and the foothills of the Brandberg, showed highly contrasting results (Von Willert & Wagner-Douglas 1994) which allow no generalizations to be made about adaptations.

9.4.5 Succulents

Succulents, defined by their ability to store water (Von Willert *et al.* 1990), form a very important part of the flora of the Namib (Van Jaarsveld 1987), and include a wide spectrum of life forms (Jürgens 1986, 1990). Namib Desert succulents include annuals (e.g. *Zygophyllum simplex*, summer-rainfall annual), ephemerals (e.g. *Mesembryanthemum guerichianum*), pauciennials (*Mesembryanthemum squamulosum*, *Sphalmanthus* spp.) and perennials (*Ruschia* spp.). Tall stem-succulents are the dominant succulent growth-form in the Nama-karoo portion of the desert biome. However, leaf succulent chamaephytes with a minor admixture of stem succulents that are either small (e.g. *Euphorbia stapelioides*) or thin-stemmed (e.g. *E. chersina*) predominate in the succulent karoo portion of the biome (Jürgens 1986; Chap 7, this volume). Ecologically, this pattern of separation can be explained by the more opportunistic behaviour of the small succulents of the succulent karoo, which are able to take up water from fog or even humid air, but require regular water availability for long-time survival (Von Willert *et al.* 1992) compared to the larger and more drought-resistant stem-succulents with their larger water-storage volumes. Therefore, tall stem-succulents are better adapted to the less predictable rainfall pattern of the Nama-karoo (Hoffman & Cowling 1987). However, the concentration of tall stem-succulents in regions with a mean daily maximum temperature in the hottest month of more than 32.5 °C suggests that hot climates may favour this growth-form (Jürgens 1986).

Highest growth-form diversity of succulents is found in the succulent karoo portion of the desert biome (see also Chap.7, this volume). Here, many species belonging to the same growth-form (e.g. dwarf leaf-succulent shrubs) may coexist in small sites (Cowling *et al.* 1994). Despite their similar appearance, many of these leaf-succulents are not functional analogues, but respond differently to drought conditions (Cowling *et al.* 1994). For example, leaf-succulent Mesembryanthemaceae and Crassulaceae have very different leaf anatomies and phenological rhythms (Jürgens 1985,1986,1990), resulting in different responses to extreme droughts (Von Willert *et al.* 1985,1992). These differences should be incorporated into any functional group classification of desert plants (Jürgens 1986, 1990).

9.4.6 Psammophorous plants

There are many Namib Desert species, termed psammophorous plants, which accumulate a cover of sand and dust, thereby forming a protective layer against the destructive force of sand storms (sand blasting) (Jürgens 1995). In some cases sand grains are fixed by a sticky substance covering most of the leaf surface (e.g. *Psammophora nissenii*), in others, sand grains adhere to sticky hairs or glands borne on only certain parts of the plant surface (e.g. *Monechma* spp.). A preliminary analysis of the phytogeographic distribution of psammophorous plants shows a clear concentration in the southern Namib Desert (N. Jürgens, unpubl. data), a region with the strongest winds and the highest sand transport rate in southern Africa (Lancaster 1985). Psammophorous species such as *Psammophora nissenii*, *P. modesta* and *Chlorophytum viscosum* are important constituents of the vegetation in the Diamond Area No. 1. Many other structural features, e.g. the subterranean growth of *Fenestraria rhopalophylla*, also provide protection against the strong sand blasting. It is a remarkable fact that psammophorous plants are extremely rare outside the Namib Desert. Furthermore, in these rare examples (e.g. *Silene viscosa* and *Ifloga spicata* in the Mediterranean Basin) the ability to fix sand to their surface is not as strongly developed as in the Namib species. The rarity of this adaptation at a worldwide scale can be explained by the fact that, usually, sand blasting takes place only in very extreme deserts, which are devoid of vegetation. In the southern Namib, however, fog, high humidity and low temperatures support rich vegetation in a virtually rainless environment where sand blasting is a frequent occurrence.

9.5 Ecophysiology

9.5.1 Modes of carbon dioxide fixation

All three photosynthetic pathways (C_3, C_4 and CAM) are present in Namib Desert plants (Von Willert *et al.* 1992). Among succulents the most common photosynthetic pathways are the CAM and C_3 types whereas the C_4 type is restricted to some halophytic succulents and a few annuals such as *Zygophyllum simplex*, which occur in dry areas with summer rainfall (Von Willert *et al.* 1992; see also Chap. 16, this volume). Some desert plants exhibit two photosynthetic pathways, following each other in an ontogenetically controlled sequence: for example, the leaf-succulent *Mesembryanthemum crystallinum* switches from C_3 to CAM (Herppich, Herppich & Von Willert 1992). There is a direct relationship between rainfall regime and photosynthetic pathway in the grasses of the Namib Desert and in southern Africa in general: C_3 grasses occur predominantly in the winter-rainfall region and C_4 grasses in the summer-rainfall region (Ellis, Vogel & Fuls 1980).

9.5.2 Water uptake

Many desert plants have developed additional means of water uptake besides uptake by roots. Water can be taken up directly via leaf or stem surfaces. For example, several species of *Crassula* take up water through their leaves (Barthlott & Capesius 1974) via specialized exposed structures, referred to as hydathodes (Tölken 1985; Von Willert *et al.* 1992) or adsorption fissures (Jürgens 1985, 1986). Von Willert *et al.* (1992) showed that many Mesembryanthemaceae are able to regain nearly 50% of their daily water losses by transpiration during the following night, provided a clear sky allows sufficient cooling of the leaf surfaces. Under these circumstances and with sufficient humidity, 'reverse transpiration' seems to be possible for plants under drought stress or with very negative osmotic potentials. Thus, water uptake is driven by a reversed water vapour gradient that can be directed from the atmosphere into the substomatal cavities of leaves. This may be one advantage of the accumulation of salts observed in most Mesembryanthemaceae (Von Willert *et al.* 1992). Uptake of fog water by the stems of the halophilic *Arthraerua leubnitziae* has been confirmed by ecophysiological observations (K. Loris, pers. comm.) and water uptake from fog by *Trianthema hereroensis* has been observed in the central Namib dunes (Seely, De Vos & Louw 1977; Nott & Savage 1985).

9.6 Community structure and dynamics

9.6.1 Phenology

The phenology of most desert plants is closely related to rainfall, temperature and soil moisture. However, some species flower at any time of the year, provided there is sufficient rainfall (Von Willert *et al.* 1992; Günster 1994b). Other species show a photoperiodic response and only flower at certain times of the year (Ackerman & Bamberg 1974). Both strategies are present in the Namib, sometimes within the same species, and depending on climatic conditions at a particular site. Inland populations of the evergreen desert shrub *Calicorema capitata*, for example, have a distinct flowering period independent of the rainfall pattern in a particular season, whereas coastal populations of the same species flower all year round, apparently because of the continuous moisture supply (M.K. Seely, unpubl. data).

9.6.2 Seed biology and germination

Little work has been done on seed biology, germination and dispersal of Namib desert plants. Life histories and reproductive strategies differ in the summer and winter rainfall portions of the Namib. In the northern and central Namib with predominantly summer rains, plants respond directly to the amount of moisture provided and germinate readily as soon as a certain soil moisture level is reached (Günster 1994b). In the southern Namib, besides rain, temperature and photoperiod play an important role in germination (Van Rooyen & Grobbelaar 1982). Another important factor determining the dynamics of desert plant communities is the minimum amount of precipitation required to trigger germination. Grasses on the central Namib plains germinate after 17 mm of precipitation (Seely 1978a), whereas trees and shrubs require more moisture. *Welwitschia mirabilis*, for example, germinates after 25 mm of rain (Bornman 1972). Besides the minimum amount of moisture, seed dispersal mode can also influence germination patterns. In serotinous species in the central Namib, seeds that are ballistically dispersed germinate earlier than those that are dispersed by raindrops (Günster 1994b).

The frequent but low moisture supplied by fog along the coast also affects germination patterns. Populations of the same annual species in the southern Namib showed different dormancy periods, depending on whether they grew inland or near the coast (Hartmann 1983). The coastal populations showed a longer dormancy period, thus preventing germination after heavy fog, which might provide sufficient moisture to trigger germination, but not enough for seedling establishment.

Dormancy and germination behaviour are usually variable within and between species, sometimes even between seeds positioned on different parts of the same plant. These are strategies to spread the risk of unsuccessful seedling establishment in a particular season. There are several annuals and perennials in the northern and central Namib that show this behaviour (Stopp 1958; Marsh 1987, Günster 1995b) and which warrant further investigation. In an annual *Mesembryanthemum* sp. from the southern Namib, not more than 27% of seeds germinated after 80 days (Ihlenfeldt 1985). In contrast, a perennial succulent, ~~*Delosperma pergamentaceum*~~, germinated rapidly after rains and most seedlings emerged at the same time, thus indicating a relationship between life-history strategy and germination pattern (see also Chap. 7, this volume).

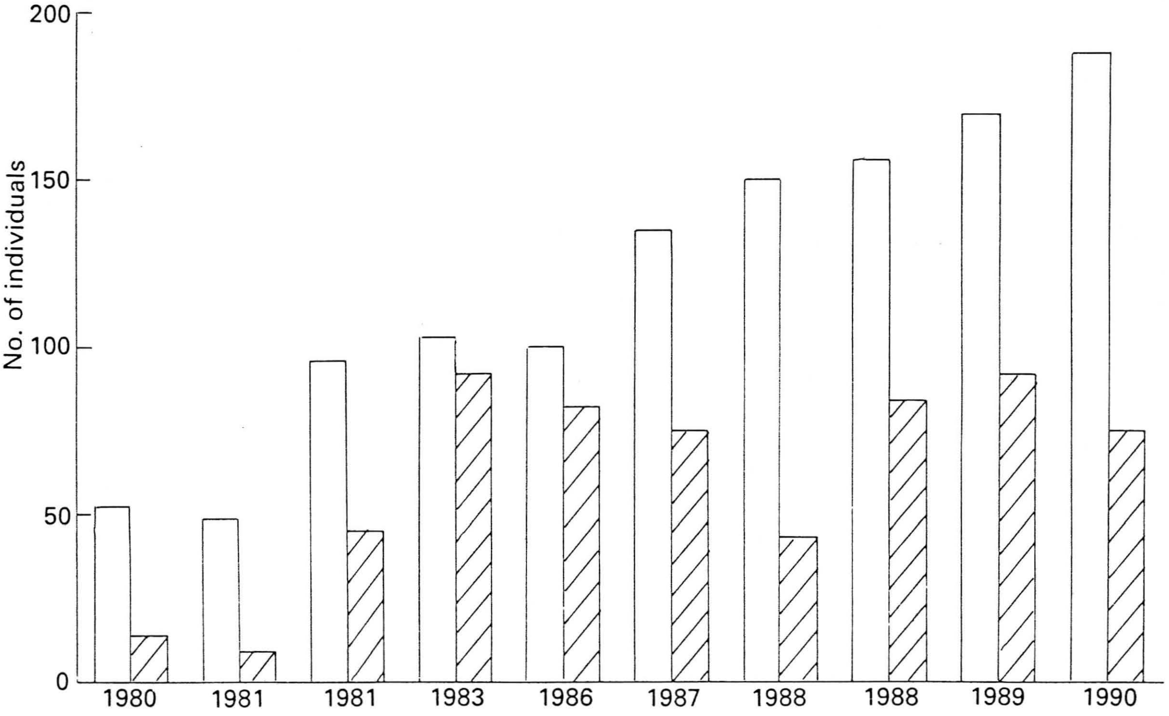
Some species are adapted to the environmental conditions that prevail after germination. During germination in these groups, e.g. the Mesembryanthemaceae, a seed lid (operculum) covers the radicle, which remains protected by the inner integument for some time (Bittrich & Ihlenfeldt 1984). If dry conditions continue for a number of days, the seed suspends germination until favourable conditions return.

After germination, numerous environmental factors including microtopography, soil moisture and nutrient conditions, as well as competition with other seedlings determine levels of establishment. Survival rates are highly variable within and between species. On the eastern Namib plains, survival rates fluctuate between zero and 100% in different seasons. Rainfall patterns, determined by the timing, spacing and intensity of rain events, are important factors influencing seedling establishment. In the eastern Namib, early rains in summer result in lower seedling survival than later rains in autumn, when temperatures are lower and evaporation rates are reduced (Günster 1994a,c).

Hartmant. pergamenceus (recent name change)

As for perennial plants, even-aged stands of shrubs indicate that establishment of shrub seedlings occurs only in particularly good seasons which, in most arid

Figure 9.15. **Increase in the number of individuals in a permanent observation plot in the Richtersveld over a period of ten years after the drought of 1978 and 1979. Two life-form groups are shown: white bars, chamaephytes with evergreen succulent leaves with a xeromorphic epidermis, showing a continuous recovery; hatched bars, chamaephytes with annually shed succulent leaves with mesomorphic epidermis (with bladder cell idioblasts), showing a more opportunistic response to rainfall.**



parts of the Namib, might be once in decades. The same is true for the perennial dune grasses (Seely 1991) and trees in ephemeral water courses (M.K. Seely, pers. obs.).

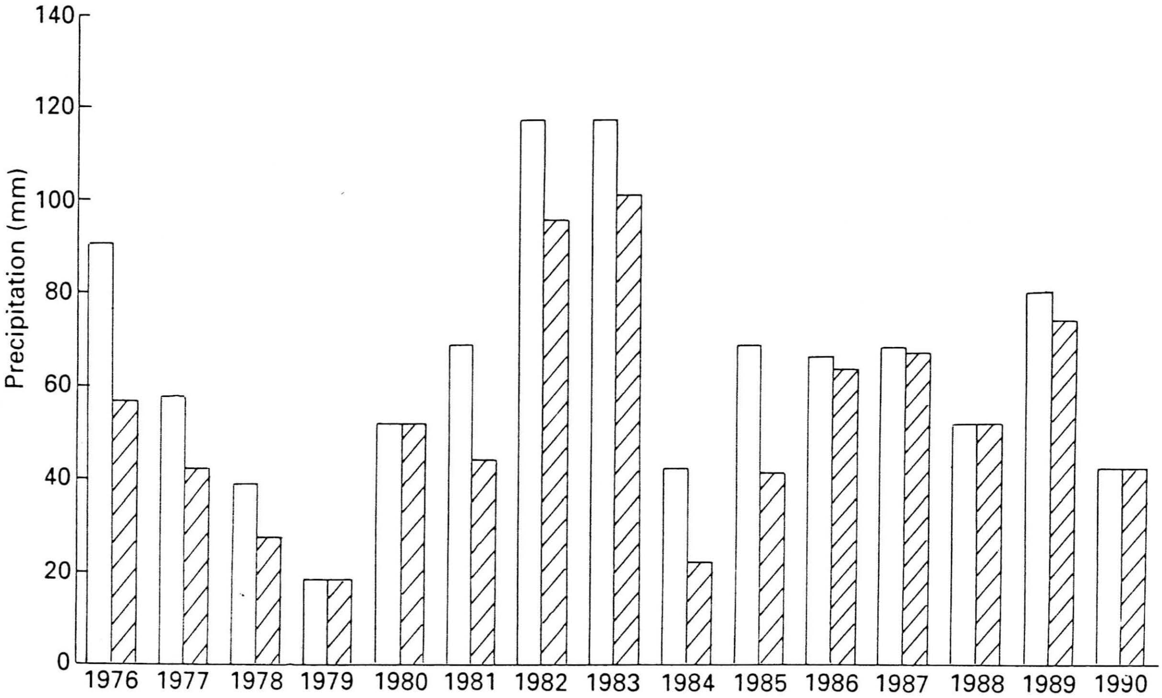
Seed dispersal has a crucial impact on community structure and dynamics. As in many other deserts, harvester ants in the Namib gather seeds in their nests and leave most behind when they move to another site (Marsh 1987). Plants that retain seeds on the parent plant for several seasons are common in many parts of the eastern Namib (Günster 1994c). It has been proposed that these seed-retaining or serotinous plants are abundant in the eastern, central Namib, because of unpredictable and intense rains as well as seed predation by insects and small mammals (Günster 1992). To increase the chances of distributing seeds to favourable microhabitats, several plant species show dimorphic dispersal strategies. *Geigeria alata*, for example, is a facultative perennial that produces diaspores adapted for short-range dispersal and diaspores adapted for long-range dispersal (Günster 1995b). The Namib is similar to other deserts (Ellner & Shmida 1981) in having a hign incidence of species with special adaptations for seed dispersal (Ihlenfeldt 1983; Günster 1992).

9.6.3 Population dynamics

There are no long-term studies of populations of Namib plants. However, short-term fluctuations in composition of annual species were observed in the eastern Namib in response to variation in the timing and amount of rainfall: these were associated with different dormancy and germination behaviour of the species involved (Günster 1993c, 1994a).

Climatic oscillations at a scale of several years can have a clear effect on the composition of the vegetation, as was demonstrated in the northern Richtersveld. Monitoring of a 100-m^2 permanent plot at the end of each winter growing season showed that species composition did not change significantly over a ten-year period (1980–1990) (N. Jürgens unpubl. data). However, massive changes in biomass and number of individuals of different species and of life-form types were observed (Fig. 9.15). These changes were determined by rainfall patterns: lower than average rainfall was recorded from 1977 to 1980, followed by wet years from 1981 to 1983 (Fig. 9.16). Over the monitoring period there was a steady increase in individuals of leaf-succulent chamaephytes which have a xeromorphic epidermis. These evergreen

Figure 9.16. **Precipitation in the Richtersveld (Lekkersing) 1976–1990, showing drought situation in 1978 and 1979. Precipitation shown for year (white bars) and winter (hatched bars).**



plants provide safe sites for germination for many other species (Jürgens 1986). This increase is interpreted either as a period of recovery after the dry period or as the response of vegetation to a climatic oscillation. The number of individuals of leaf-succulents, which possess a mesomorphic epidermis (i.e. an epidermis with thin-walled bladder-cell idioblasts) and which shed their leaves during the dry season (Jürgens 1986) also increased in 1981. However, the number of individuals remained fairly constant thereafter. This group behaved more opportunistically and established numerous individuals in the years with the highest winter rains (1983 and 1989). Oscillations in the density of annuals and geophytes were extreme and these two groups showed different responses to the rains of the different years. Both groups increased in the good rain years of 1983 and 1989.

9.6.4 Species interactions

The role of competition in determining the structure of Namib Desert communities ranges from weak to strong, depending on the habitat and the climatic region. Competition for water and nutrients is important in structuring the hyper-arid communities on dunes (Yeaton 1990), and is probably of increasing importance towards the eastern Namib, where higher rainfall results in denser vegetation (Polis 1991). Nothing is known about other communities in this respect.

Namib desert plants support a variety of consumers, ranging from seed-eating insects, birds and small mammals to large browsers and grazers such as ostrich, antelopes, elephants and black rhinoceros (Stuart 1975; Seely & Louw 1980; Loutit, Louw & Seely 1987; Viljoen 1989). Although large-scale movements of game species in response to rainfall and consequently primary production have been recognized (Tarr & Tarr 1989), very few quantitative data are available on their impacts on plant communities. Elephants in the northern Namib, for example, have had no detrimental effect on the tree populations in the rivers over the last 20 years, although their food preferences for species such as *Faidherbia albida* might affect the composition of the riverine vegetation in the long term (Viljoen & Bothma 1990).

An association between a leaf- and a stem-succulent species has been reported from the Namib gravel plains (Dean *et al.* 1992). This study showed that seedling establishment of the stem-succulent *Euphorbia damarana* was confined to sites in the shelter of the leaf rosette of *Aloe asperifolia*. Many more associations of this type are expected between different species and in different parts of the Namib, e.g. between *Salvadora persica* and *Boscia foetida* in Damaraland (A. Günster, pers. obs.). In the Richtersveld, beneath adult individuals of low evergreen leaf-succulent chamaephytes, up to five species are regularly found. Furthermore, about 80% of the newly established individuals (less than one year old) of perennial Mesembryanthemaceae had established beneath these nurse plants (N. Jürgens, pers. obs.).

9.7 Ecosystem function

Although a direct relationship between rainfall and annual grass production has been recognized in the Namib (Seely 1978a,b; Günster 1995c), there have been no studies on the productivity of the perennial vegetation. In general, productivity increases with increased moisture availability. Yeaton (1988) showed that the standing crop of *Stipagrostis sabulicola* increases in an easterly direction with increasing rainfall across the Namib dunefield, as does the average standing crop of the dunegrass communities. The average standing crop of individuals in dune slope communities is also highest on the mid- to lower dune slope, where moisture conditions are optimal (Yeaton 1988).

Namib dune sand is deficient in all three macronutrients: nitrogen, phosphorus and potassium (Seely & Louw 1980; Jacobson 1992). Mycorrhizal fungi are well known for improving plant growth under low-nutrient conditions (see Chap. 16, this volume) and have well-developed associations with grasses in the Namib dunefield (Jacobson 1992). The role that these fungi play in nutrient cycling in the Namib Desert has not yet been investigated. However, it is generally known that in addition to improving nutrient and moisture relations of the plants the activities of fungi support other organisms in the plant rhizosphere (Allen 1991; Chap. 16, this volume).

Detritus from dune plants represents a largely aseasonal, relatively persistent form of organic matter in mobile dunes, on which many organisms depend (Louw & Seely 1982; Crawford & Seely 1993). Detritivores are generally more abundant than carnivores in the Namib dunes, even though similar numbers of species exist (Crawford & Seely 1987). Arthropods probably decompose the most plant detritus in the Namib Desert, but the role that micro-organisms play in the decomposition and mineralization of detritus and litter has not yet been investigated. Fungi are ubiquitous following rain events and, as with plant species, their activity patterns are synchronized with optimal utilization of available moisture (P. Jacobson, unpubl. data). Information concerning interactions between micro-organisms, the material that they decompose, and other organisms involved in decomposition, are lacking for the Namib

Desert. Some studies in other deserts suggest, however, that termites may preferentially consume plant material colonized by fungi, because of the higher carbon : nitrogen ratios resulting from fungal decomposition of the plant substrate (West 1991). *Psammotermes mossambicus* has been observed eating this high-quality equivalent in the Namib dunes (Crawford & Seely 1994; K. Jacobson, pers. obs.), but how important this is to nutrient acquisition by the termites is not known. As termites are thought to be major consumers in the Namib Desert (Crawford & Seely 1994), such interactions may have important implications for nutrient cycling and deserve further study.

9.8 Management and human use

9.8.1 Desertification

Hunter-gathering and nomadic pastoralism were the primary land uses for the Namib Desert up to the last century (Kinahan 1991). There is ample evidence that much of the plains landscape was used on an irregular basis, presumably after good rains. More recently, parts of the eastern fringe of the Namib have been used for emergency grazing during drought by commercial farmers. Today, communal farmers on the desert borders use the perennial vegetation during drought periods and permanent settlements are being established on the desert fringe. These communal farmers are particularly dependent on the vegetation of the ephemeral river courses (Jacobson *et al.* 1995). As the populations in the communal areas increase, so their activities extend further into the Namib. In contrast, many of the private farmers owning land on the desert edge are abandoning livestock farming and focusing on tourism and other alternative development strategies. Nevertheless, overgrazing appears to be of growing concern as farmers under all land-tenure systems fail to adjust stocking rates to the natural wet and dry cycles (Seely & Jacobson 1994). High proportions of unpalatable and poisonous plant species in the current vegetation are a clear indicator of incipient degradation (Günster 1993a).

9.8.2 Tourism

Tourism in Namibia is rated as one of the three top earners of foreign exchange before the turn of the century (Hoff & Overgaard 1993). The Namib Desert, along with wildlife throughout the country, is a major tourist attraction and the sand dunes such as those at Sossusvlei are popular destinations. Part of this attraction is the dune vegetation, seen to be thriving in an extremely hostile environment. This attraction could be enhanced by information for tourists on the natural history of the endemic plants and animals (Seely 1987).

Further tourist attractions in the desert are the linear oases provided by the large trees growing along the ephemeral river courses (Jacobson, Jacobsen & Seely 1995). These trees provide browse and pods for wildlife as well as shade for tourists. Their conservation status is, however, affected by activities in the higher catchment areas. The mountains of the Namib, for example the Brandberg and to a lesser extent the Naukluft Mountains, are also foci for tourism and recreation. The unusual succulent flora of the high Brandberg is particularly interesting to visitors. Less well-protected coastal areas of the Namib are also used by tourists and fishermen, although the coastal vegetation is subjected to heavy vehicular traffic (Seely 1987).

Tourism in the Namib is supported by the Government of Namibia in that the entire core desert, lying between the Kunene River in the north and Lüderitz in the south, is incorporated into protected areas: the Skeleton Coast Park in the north, the West Coast Recreation area in the centre and the Namib–Naukluft Park to the south. With the exception of a narrow coastal strip, the entire Sperrgebiet (Diamond Area) south to Lüderitz is also a protected area. Within these protected areas, some land is managed as private tourist concessions with long-term government contracts. Adjoining the protected areas, many private farming concerns are developing guest farms where tourists can enjoy the local environment or travel to state-controlled tourist areas. Similarly, community-based tourist camps are also situated to take advantage of the desert landscape and state-controlled land. In the state-controlled communal lands inland from the coast, community-based game guards at present play a major role in maintaining the integrity of the landscape and its wildlife. Tourism, present and future, is enhanced by their efforts and those of their supporting non-government organizations. Nevertheless, conflicts over land and water use in this area are escalating.

9.9 Conclusions

Although the Namib has been the focus of much botanical interest, scientific research on the vegetation has been limited. More research is required on all aspects of the biome's flora and vegetation. More taxonomic research is still required in a number of taxa, e.g. Mesembryanthemaceae and various petaloid monocots (see also Chap. 7, this volume). Distribution data for species and vegetation units are also inadequate. Basic knowledge on important environmental parameters, e.g. fog precipitation, is missing. Very few sites for the analysis of vegetation dynamics have been established in this highly variable environment. Few data are available on species interactions, life-history strategies or soil-plant interactions, and comprehensive ecosystem-level studies have yet to be initiated. Data are lacking on the history of the desert environment, especially with respect to changing patterns of human influence. Studies on desertification processes and the potential for restoring degraded environments are in their infancy. It would be a great tragedy if the unique flora and vegetation of the Namib Desert were to remain so poorly known and understood.

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