Reprinted from: *Hot Deserts and Arid Shrublands, B* edited by M. Evenari et al.

A.N.W. Rpt

Chapter 7

With best compliments
H. Walter

THE NAMIB DESERT[1]

H. WALTER

With contributions by W. Giess, H. Scholz, H. von Schwind†, M.K. Seely and E. Walter

INTRODUCTION

Southern Africa lies between 17° and 35°S latitude, and therefore is within the arid subtropical belt, with the exception of its southernmost part. The warm Moçambique Current in the east and the cold Benguela Current in the west give rise to a pronounced gradient of humidity from east to west. A cross-section through southern Africa along the Tropic of Capricorn looks like a section through an inverted dish. The middle part is slightly depressed, forming the large Kalahari Basin filled with sand. The margins — the Drakensberge in the east (up to 3000 m high) and the high plateau of Namibia, or South West Africa (up to 2000 m high) in the west — are raised and form a steep escarpment towards the coast (Fig. 7.1A). In the south the high Plateau slants downward, forming a number of steps. Between the steps lie the basins of the Great and the Little Karoo.

Because of its latitude, South Africa is exposed in summer to the easterly trade winds. They carry air masses which take up large amounts of water vapour when passing over the warm Moçambique Current. When these winds rise on the eastern slopes of the Drakensberge, the greater part of their moisture is precipitated. Consequently the air farther west is much drier. More moisture is lost in thunderstorms and therefore precipitation decreases progressively toward the west. The winds blowing up the slopes of the Western Highlands do not create any noticeable rains, and the Namib on the Atlantic coast is a rainless desert. The special conditions of the Namib brought about by the presence of the cold Benguela Current will be dealt with later.

This account shows that the Kalahari has a higher precipitation than the settled farmland lying to its west (Fig. 7.1B). The Kalahari is, in the north, a savanna forest with deciduous trees, changing towards the south with decreasing precipitation into a shrub savanna (Leistner, 1967; Leistner and Werger, 1973). The plant cover everywhere in the Kalahari is almost closed because its sandy soils guarantee a good water supply. The Kalahari is therefore neither a desert nor a semidesert as it has been thought to be. It is a "thirstland" because the rain drains off in the sand to such a degree that there are only a few water holes supplying drinking water. The Kalahari will therefore not be dealt with here. The most arid parts of southern Africa are rather the Namib along the Atlantic coast, and to a lesser degree the Karoo in the southern basins.

Three hundred years ago the Karoo was already settled by Europeans, being used mainly as grazing land for sheep. Consequently its vegetation was much changed, as has been especially pointed out by Acocks (1953). There are no other precise ecological investigations of the area.

The Namib was first explored in the second half of the past century, and its ecological exploration started in our century. Walter published the first ecological investigation in 1936 (see also Walter, 1971, 1973a). Logan (1960) gave an excellent geographical review of the central Namib. In 1963 Koch founded the Desert Research Station at

[1]English manuscript received May 1980. Responsible editor M. Evenari.

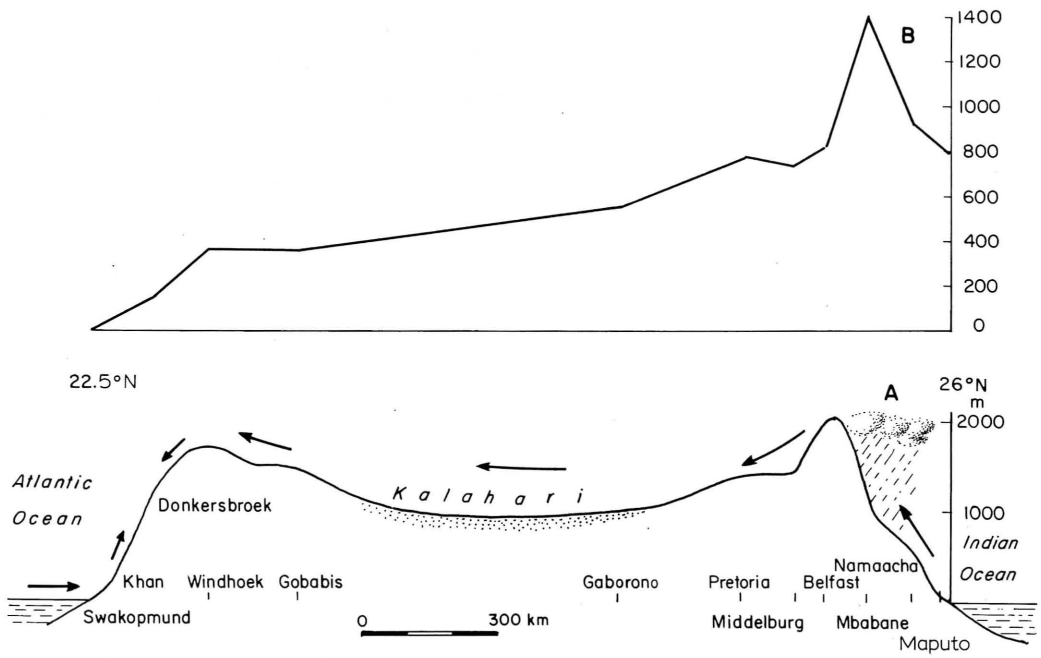


Fig. 7.1. Schematic cross-section through southern Africa from 22.5°S in the west to 26°S in the east. A. Relief with the Kalahari basin in the centre. Arrows indicate the main wind directions (mainly from SE, only on the west coast from SW). B. Mean annual precipitation (mm) along cross-section. Maxima on the east slope of the Drakensberge. Continuous decrease towards west. Precipitation in Kalahari somewhat higher than in farmland of Namibia, west coast (Namib) rainless.

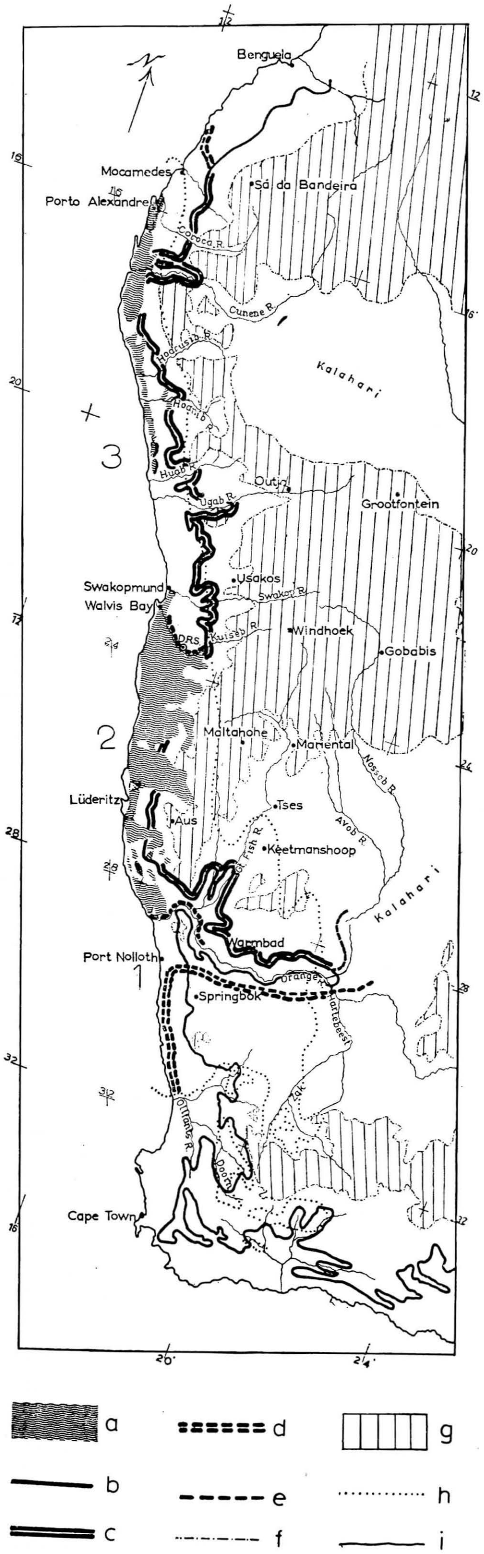
Gobabeb, which is 55 km from the coast, 100 km southeast of Walvis Bay. This has since become a centre for ecological research in the Namib; among papers recently published (listed in the Namib Bulletin, 1976) zoological and geomorphological ones predominate. The soils were investigated by Scholz (1963, 1972), weathering and geomorphological zonation by Besler (1972). Walter (1971, 1973a) dealt with the ecology of the Namib.

GEOGRAPHICAL POSITION

The Namib (Fig. 7.2) stretches from the San Nicolai River (14°20′S) in southern Angola to the Olifants River (about 32°S) over a length of almost 2000 km. However, the area south of the Orange River, Namaqualand, does not belong to the Namib proper because it receives mainly winter rain and is similiar to the Karoo.

The Namib forms a strip 80 to 150 km broad from the Atlantic coast nearly to the foot of the escarpment, rising with a gradient of 1:100 to about 1000 m. From north to south three sections can be distinguished (Fig. 7.3): (1) the northern Namib from the northern boundary to the Unjab or Ugab River; (2) the central Namib from the Unjab River to the Kuiseb River, with Sandwich Harbour (receiving Kuiseb water) 50 km south of Walvis Bay; and (3) the southern Namib to the Orange River.

The northern Namib with the Kaokoveld is ecologically hardly known. The same is true for the southern Namib, which contains large dune areas without vegetation and the closed area of diamond fields in which no investigations can be carried out. Consequently, this chapter deals only with the central Namib with Swakopmund and Walvis Bay on the coast and the Gobabeb Desert Research Station and the Namib Desert Park further inland (Fig. 7.4). Going from west to east, the central Namib can also be subdivided into three parts: (1) a narrow coastal strip; (2) the outer Namib, about 50 km wide with only episodic rain; and (3) the inner Namib with an annual precipitation of 50 to 100 mm of summer rain.



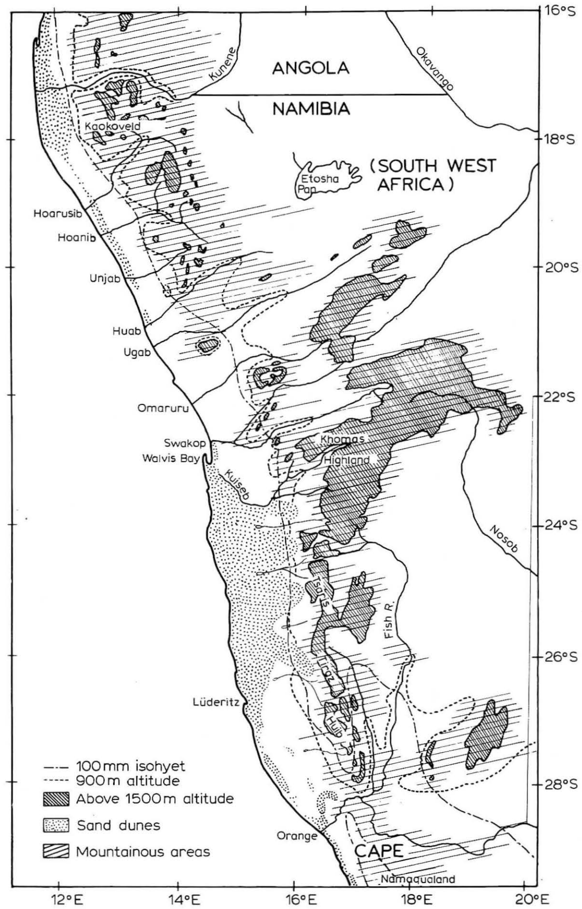


Fig. 7.3. Map of Namibia (South West Africa) (after Coetzee, 1969). The northern Namib Desert occupies the western part from Angola to the Unjab or Ugab Rivers, the central Namib south of it to the Kuiseb River (Walvis Bay), the southern Namib from there to the Orange River. Dunes extend from Kuiseb and Walvis Bay in the north to Lüderitz Bay. Sandwich Harbour is slightly south of Walvis Bay.

Fig. 7.2. Southwest coast of Africa with the desert strip (Namib) from Angola to the Olifants River in the Cape Province (after Koch, 1962a). Koch's division of the Namib is based on the distribution of tenebrionid beetles. The northern Namib of Koch corresponds to the north and central Namib of the plant ecologists.
Legend: a = barkhan dunes; b = 600-m contour; c = approximate eastern limits of the true Namib, viz. 600-m contour, except for areas where the barkhan dunes expand inland beyond it; d = northern and southern limits of the Namib Desert; e = divisions between the transitional (*1*) and the southern Namib (*2*), and the southern (*2*) and the northern Namib (*3*) (*2* + *3* = true Namib); f = 1200-m contour; g = highlands (above 1200 m); h = rainfall below 120 mm yr^{-1}; i = rivers, mostly dry; *D.R.S.* = Namib Desert Research Station.

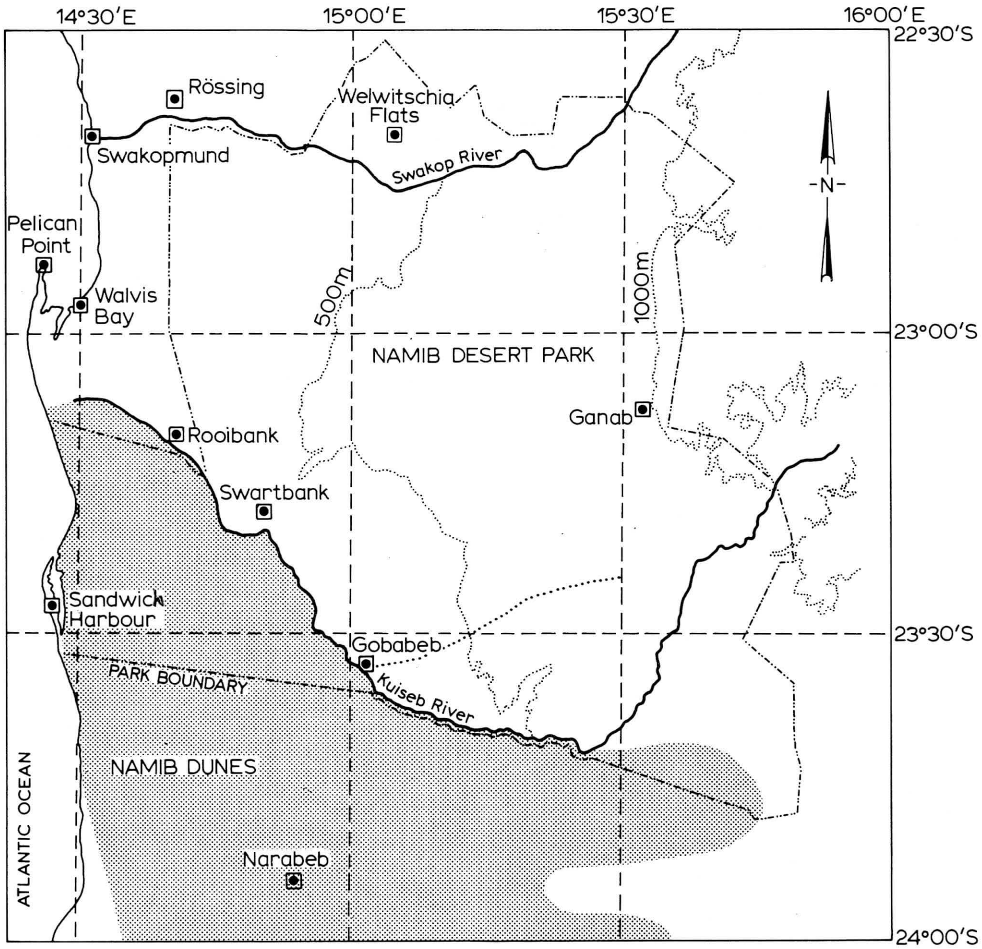


Fig. 7.4. Part of the central Namib and the dunes.

CLIMATE

General

Because of its climate the outer Namib occupies a very special position in the "hot deserts" biome. It is an extreme rainless desert but nevertheless has a very high relative air humidity and heavy wet fogs. Fluctuations in temperature are as small as in extreme oceanic climates. There are only a few days with high temperatures and no frost or hail. This is due to a permanent temperature inversion. A cold layer of air up to 600 m high lies over the cold Benguela Current and the adjacent land. It blocks the warm air currents from the east; instead a daily southwesterly sea breeze brings cool humid air.

Rainfall, fog, dew

The long-time yearly average of precipitation of the coastal stations (Table 7.1) is between 9 and 27 mm, but for deserts with only episodic rainfall the individual showers are of more importance than the yearly averages. Swakopmund is a good example. During 1931 to 1933 it had only 0.4 mm of rain in January 1931 and 4.5 mm in February 1931, but 112.9 mm in March 1934 and 26.8 mm in April of the same year — that is, 140 mm in two months! The effect of such an extreme rainy year, which occurred only once in this century, extends over decades. Normally, even months with more than 20 mm of rain are very rare.

The irregularity and unpredictability of the rainfall is also expressed in the enormous variation of

TABLE 7.1

Precipitation in the central Namib

Station	Coordinates	Air distance from coast (km)	Elevation (m)	Average annual precipitation (mm)	Duration of record (years)	Source
Swakopmund[1]	22°40′S, 14°34′E	2	20	18 (2.5–150.2)[3]	64	Anonymous (1944)
Swakopmund[2]				13.0 (1.4–42.8)	7	Nieman et al. (in press)
Walvis Bay[1]	22°53′S, 14°26′E	0	10	15 (0–99.3)	69	Anonymous (1944)
Rooibank[2]	23°13′S, 14°40′E	22	100	9.6 (1.3–24.1)	9	Seely
Swartbank[2]	23°20′S, 14°51′E	33	340	6.6 (0.4–18.1)	6	Seely
Narabeb[2]	23°51′S, 14°57′E	40	410	3.0 (0.8–7.1)	3	Seely
Welwitschia Flats[2]	22°40′S, 15°02′E	53	420	11.3 (3.0–17.3)	3	Seely
Gobabeb[1]	23°34′S, 15°03′E	56	410	15.6 (0.0–26.3)	13	Weather Bureau, Pretoria
Gobabeb[2]				14.1 (2.2–30.3)	10	Seely
Ganab[2]	23°10′S, 15°32′E	110	1000	63.8 (6.1–173.5)	8	Seely

[1]Weather Bureau Records, standard rain gauge employed.
[2]Desert Ecological Research Unit, autographic Lambrecht gauge employed.
[3]The figures in brackets are the lowest and highest ones observed during the recording period.

precipitation from year to year (Tables 7.1, 7.2). In Gobabeb and Walvis Bay, for instance, there have been years with zero precipitation, as against years with 100 mm of rain. In the coastal and outer Namib, most rains fall in the summer, thus intensifying the aridity (Seely and Stuart, 1976). These summer rains occur when there is no temperature inversion and no sea breeze. Then the warm and humid air from the Indian Ocean penetrates downwards. Consequently, the strong heating of the lower air mass leads to thunderstorms. The probability that both conditions causing thunderstorms and rain occur simultaneously are greater in summer and further inland. Thus, the average precipitation increases with increasing distance from the sea, from nearly zero to about 100 mm on the eastern border of the Namib.

TABLE 7.2

Precipitation at Gobabeb and Ganab (mm yr^{-1})

	Gobabeb (23°34′S, 15°03′E; 410 m)	Ganab (23°10′S, 15°32′E; 1000 m)
1965/66	2.2	–
1966/67	26.8	–
1967/68	5.4	15.4
1968/69	30.3	124.3
1969/70	3.5	6.1
1970/71	20.7	44.2
1971/72	25.2	70.9
1972/73	8.1	62.5
1973/74	23.6	173.5
1974/75	7.1	13.1

Conditions in the southern Namib and Namaqualand are different. Precipitation there is tied to the occurrence of moving cyclones which in winter transgress even Lüderitz Bay. Rain in the southern Namib is therefore winter rain.

Besides this measurable precipitation, the Namib is characterized by fog and dew which cannot be measured exactly. In the opinion of many they have greater biological importance than rain. In Swakopmund fog occurs very frequently. This is related to the presence of a fog bank which almost permanently overlies the Benguela Current. Its temperature on the surface is about 12°C, whereas the temperature of the ocean water at a distance of 300 km from the coast is from 16 to 20°C (Marchant, 1929, quoted by Logan, 1960). The Benguela Current starts west of the Cape as a small band and moves with a velocity of 40 km day^{-1} northward. At the mouth of the Orange River it is already 150 km wide and becomes even wider as it moves north.

The sea breeze carries the fog from the sea towards the land where it moves slightly above the soil surface, creating a very light and fine rain (*Nieselregen*). The fog dissolves slowly during the day as the soil is heated up by radiation penetrating through the fog.

This "moving fog" (*Treibnebel*) must be differentiated from the "ground fog" (*Bodennebel*) further inland, which is created during the night, just on the soil surface, by the strong outgoing radiation from the soil.

The ground fog and the dew produced by it are also favoured by the sea breeze, which raises the air humidity over the desert. The borderline between dry eastern and humid western air moves continuously in both directions and results in the rapid changes in temperature and humidity which are so characteristic of the Namib.

Nobody has so far paid attention to how far inland the moving fog reaches and where the ground fog starts. Logan (1960) observed during a night journey through the Namib to the coast that ground fog prevailed between 68 and 36 km from the coast, then a short stretch was clear of fog, followed towards the coast by advective moving fog.

It is therefore obvious why the monthly distribution of fog days differs between Swakopmund (moving fog) and Rössing (40 km from the coast; mostly ground fog) (Table 7.3).

It is important to differentiate between the two types of fog in order to evaluate the amount of fog precipitation (including dew), which is usually over-estimated. In Swakopmund 257 l of water from fog was collected from a slightly inclined house roof of 60 m^2 over a period of 35 days of which 21 were foggy days. This is seemingly a large quantity but amounts only to an average of 0.2 mm per foggy day, with a range of 0.01–0.7 mm. These values agree well with results obtained with Leick dew plates during 57 measuring days (Walter, 1936). In other fog and dew areas no values higher than about 1.0 mm have ever been observed.

The situation is very different when moving fog encounters a vertical obstacle. In this case the quality of the obstacle, the wind velocity and the degree of oversaturation of the fog are decisive. The highest amounts of water from fog are obtained when the obstacle has a large surface and at the same time transmits wind as, for instance, the crown of a tree which "combs out" the droplets of fog, turning them into drops of water.

The fog gauges used lately in the Namib, which consist of a rain gauge above which a cylinder made of fine mesh is placed, do not transmit enough wind. A rain gauge with a bundle of vertical thin rods above it could be a better standard fog gauge.

Fog precipitation on an even soil surface in Swakopmund could possibly amount to 40 to 50 mm yr^{-1} according to very incomplete measurements. In Gobabeb a yearly average of 35.2 mm of precipitating fog has been measured over a ten-year period (Table 7.4). In comparison with the amount of rain these seem to be high values. But since the 40 to 50 mm in Swakopmund fall in about 200 days, the average daily amount is 0.2 to 0.7 mm (Walter, 1936). The corresponding average figure for Gobabeb is 0.9 mm day^{-1}. As a water source for plants these small amounts would be of importance only if they were taken up directly (see below).

TABLE 7.3

Number of days with fog in 1914 (Walter, 1936)

Month	Swakopmund	Rössing
Febr.	5	28
March	10	23
April	15	7
May	27	10
June	21	12
July	9	9
August	8	24

TABLE 7.4

Mean number of fog days and amounts of fog, measured over a ten-year period (1962–1972) at Gobabeb (Seely and Stuart, 1976)

Month	Days with fog precipitation	Fog amount (mm)
January	1.7	0.8
February	3.3	2.8
March	3.8	3.4
April	1.7	2.5
May	1.7	1.5
June	2.2	2.8
July	3.4	3.9
August	3.8	4.9
September	4.6	4.1
October	5.0	4.4
November	3.0	1.6
December	3.0	2.5
Total	37.2	35.2

TABLE 7.5

Temperatures (°C): mean monthly and annual maximum (upper row), minimum (middle row) and mean (max + min/2, lower row) and absolute maxima and minima measured at six Namib stations (Fig. 7.4) (after Besler, 1972; Seely and Stuart, 1976)

Jan.	Febr.	March	April	May	June	July	August	Sept.	Oct.	Nov.	Dec.	Year	Absolute maximum	Absolute minimum
Swakopmund														
20.8	20.9	20.3	17.7	17.5	18.6	18.4	15.5	16.4	17.2	19.1	20.5	18.6		
15.9	16.0	16.1	12.8	11.8	10.0	10.0	9.6	10.8	11.3	14.4	15.7	12.9	35.4	3.1
18.4	18.5	18.3	15.3	14.7	14.3	14.3	12.6	13.6	14.3	16.8	18.1	15.8		
Walvis Bay														
23.6	23.2	23.6	22.2	25.0	22.7	18.3	18.9	18.4	20.4	21.6	22.3	21.7		
15.6	15.9	14.9	13.4	12.1	11.4	7.6	9.0	10.8	12.0	12.6	14.2	12.5	38.0	2.1
19.6	19.6	19.3	17.8	18.6	17.1	13.0	14.0	14.6	16.2	17.1	18.3	17.1		
Rooibank														
25.6	26.2	27.6	26.0	27.0	24.2	23.9	23.0	24.1	23.9	25.8	25.2	25.2		
14.7	14.9	14.6	11.0	10.8	8.6	7.2	7.3	8.8	10.0	12.2	13.5	11.1	40.3	−0.2
20.2	20.6	21.1	18.5	18.9	16.4	15.6	15.2	16.5	17.0	19.0	19.4	18.2		
Swartbank														
28.9	29.0	32.0	30.5	30.3	26.2	26.2	26.1	26.5	26.3	28.5	27.9	28.2		
13.9	14.2	14.6	12.2	11.6	8.7	8.3	7.6	7.8	9.0	11.0	11.9	10.9	39.5	0.0
21.4	21.6	23.3	21.4	21.0	17.5	17.3	16.9	17.2	17.7	19.8	19.9	19.6		
Gobabeb														
31.4	31.9	33.3	31.8	30.1	26.6	26.7	27.4	29.3	29.1	30.7	30.8	29.9		
15.3	15.1	16.2	14.6	13.5	10.9	10.0	9.7	10.2	10.9	12.3	13.1	12.6	42.3	1.8
23.3	23.5	24.8	23.2	21.8	18.7	18.3	18.5	19.8	19.8	21.5	22.0	21.2		
Ganab														
30.5	31.2	31.1	28.6	27.1	23.9	25.2	26.5	28.8	28.2	30.1	30.5	28.5		
17.4	18.3	19.4	15.4	13.1	11.1	12.3	12.8	14.1	12.9	18.2	18.0	15.3	40.5	2.3
24.0	24.8	25.3	22.0	20.1	17.5	18.8	19.7	21.5	20.6	24.2	24.3	21.9		

TABLE 7.6

Relative humidity of the air (%) for six Namib stations (Fig. 7.4) (from Besler, 1972)

Jan.	Febr.	March	April	May	June	July	August	Sept.	Oct.	Nov.	Dec.	Year	Period of observation
Swakopmund													
83.6	84.9	86.3	87.3	85.6	83.3	no measurements			–	88.1	84.3	85.4	Nov. '68–July '69
Walvis Bay													
75.4	77.2	73.9	74.3	63.6	63.3	74.5	76.1	80.3	78.4	77.1	77.4	74.3	Nov. '64–Jan. '67
Rooibank													
72.1	71.7	69.4	66.8	57.3	53.9	57.4	65.4	66.3	68.4	66.8	70.2	65.5	April '64–Nov. '69
Swartbank													
65.3	66.2	61.5	52.4	45.9	55.3	49.7	53.5	60.5	60.3	60.9	62.8	57.9	April '64–Sept. '69
Gobabeb													
59.2	59.6	54.6	48.4	38.7	41.6	43.4	47.8	51.2	54.5	55.0	58.2	51.0	Oct. '62–Nov. '69
Ganab													
51.8	45.5	55.8	36.6	33.7	35.3	33.9	32.9	34.8	44.2	47.5	50.3	41.9	August '67–Oct. '69

Temperature and air humidity

The basic facts are given in Tables 7.5 and 7.6. The temperature fluctuations are very small for all the stations at lower elevations as witnessed by the small difference between the mean daily temperature of the hottest and coldest month which ranges from 5.9 to 6.6°C. The corresponding figure

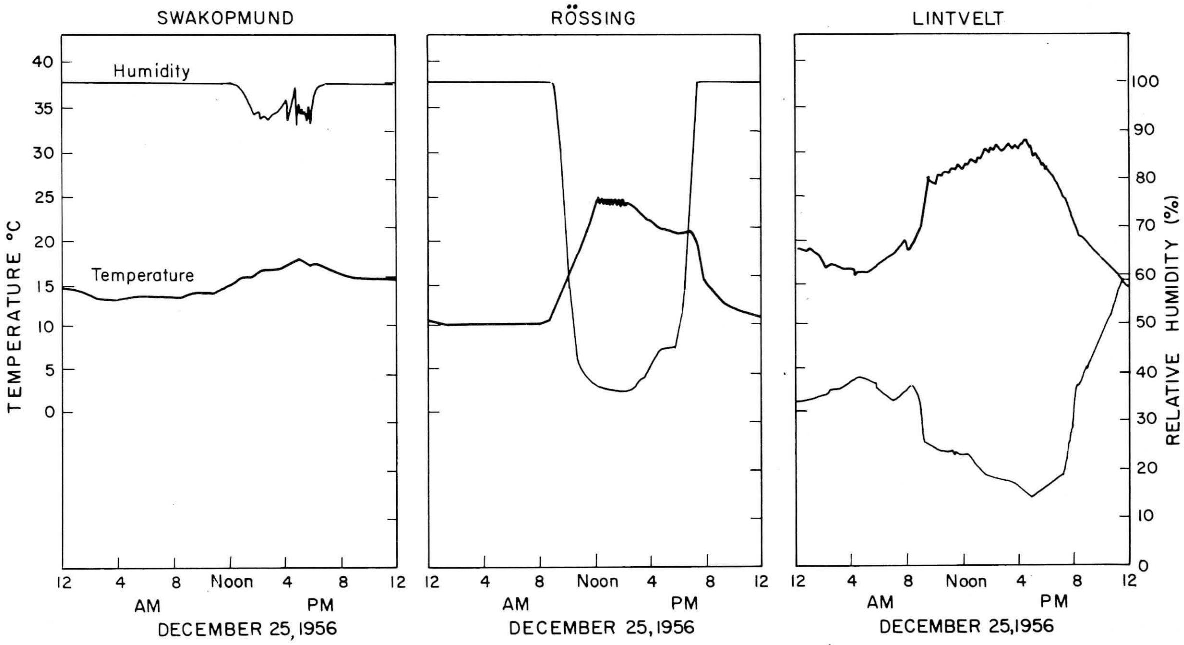


Fig. 7.5. Temperature (°C) and relative air humidity (%) on a typical foggy day (December 25, 1956) in Swakopmund, Rössing and on the escarpment near Lintvelt (modified from Logan, 1969).

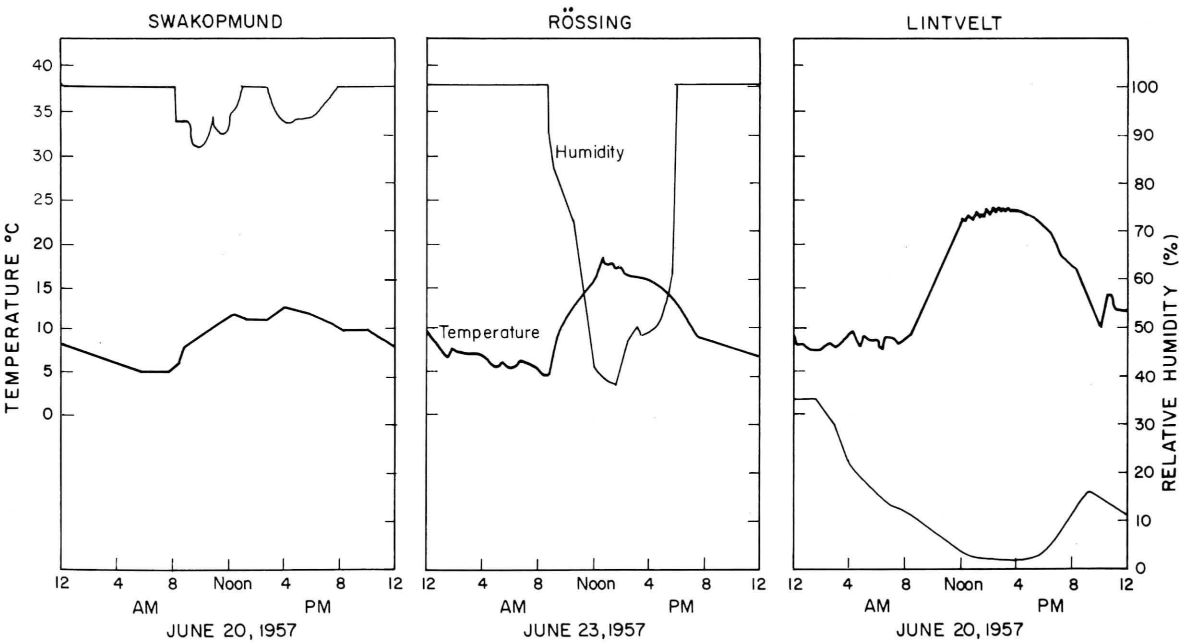


Fig. 7.6. Same as Fig. 7.5, but measurements taken on a foggy winter day (June 20, 1957) (modified from Logan, 1969).

for the Negev Desert is from 15 to 20°C. The mean yearly temperature and the absolute maxima are lowest for the coastal stations. The mean annual humidity is very high for the coastal station and decreases sharply further inland. These general data need some elaboration.

The cold layer of air above the Benguela Current and the daily sea breeze blowing inland determine to a large degree the temperature conditions of the Namib. The water content of this air is higher than that of the overlying eastern air mass. Since temperature and air humidity are closely related, they have to be treated together. Logan's (1960, 1969) observations demonstrate this clearly (see also Besler, 1972).

On two days with typical foggy weather conditions Logan carried out measurements in three different localities: (1) on the coast near Swakopmund; (2) near Rössing (40 km from the coast, 400 m above sea level); and (3) near Lintvelt (120 km from the coast, 1140 m above sea level; Figs. 7.5, 7.6).

On December 25, 1956 (summer!) the surface at Swakopmund was covered by a thick layer of fog and the air humidity during the morning was 100% at a temperature of 15°C. Later the temperature rose and air humidity decreased to 92%. At 18.00 h the temperature dropped and the air humidity rose again to 100%. At Rössing the air humidity remained at 100% only for 14 h, in contrast to the 19 h at the coast. Radiational fog was formed as a consequence of the pronounced nocturnal cooling (10°C). The high air humidity was caused by the sea breeze. At noon the temperature rose above 20°C and air humidity dropped below 40%.

On the escarpment at Lintvelt the air blown inland was hot (over 30°C) and even at midnight its relative humidity reached only 60%. Fog and dew formation on the way inland had lowered the water content.

On June 20, 1957 (winter!) the weather in Swakopmund differed little from that on December 25, 1956; only the temperature was slightly lower and the air humidity remained below 100% for a longer time. The conditions in Rössing were similar but the fog persisted there longer. The sea breeze was weaker and did not reach the escarpment any more.

However, the weather of the Namib, even on the coast, changes more than Logan's description indicated. The fog in Swakopmund, for instance, is less permanent than he reported.

There are some exceptional days in winter with *berg* (mountain) wind, when a steep gradient exists between the Highlands in the east and the sea in the west. On such days the easterly wind penetrates through the inversion layer, stirs up the hot sand and reaches Swakopmund as a veritable dust storm. On such winter days temperatures rise above 30°C and relative humidity decreases to 30 or 40%. These easterly storms cause greater sand movements than the diurnal sea breeze, which in the central Namib is not stronger than 3 to 4 Beaufort. It reaches higher values only in the south near Lüderitz Bay.

Evaporation

Evaporation in the Namib is quite high in spite of the high relative humidity and the relatively low temperatures. In Swakopmund the evaporation from basins filled with sea water for salt production was 1175 mm yr^{-1}. The evaporation in Gobabeb amounts to 3500 mm yr^{-1} (Table 7.7) — a value typical for deserts. It is most remarkable how little the monthly evaporation varies over the year (lowest value 219, highest 356; the corresponding figures for the Negev Desert are 99 and 347). The evaporation is very low on foggy days and very high on days with southwesterly storms, and especially so on days with east winds and dust storms in winter.

TABLE 7.7

Mean monthly evaporation (mm) measured with type A evaporation pan over a ten-year period (1962–1972) at Gobabeb, (from Seely and Stuart, 1976)

Month	Evaporation
January	346
February	306
March	325
April	281
May	265
June	219
July	230
August	240
September	282
October	307
November	344
December	356
Total	3501

Climate diagrams

These diagrams (Fig. 7.7) give a picture of the climatic character of the coastal region.

GEOMORPHOLOGY (by H. Scholz)

The map of the drainage system of the central Namib (Fig. 7.8) shows clearly that only the waters of the Omaruru, Swakop (with Khan) and rarely of the Kuiseb reach the sea after heavy rains have fallen on the high plateau where they originate. The waters of the many small *riviere*[1] disappear near the coast or even further inland without reaching the ocean.

The relief of the central Namib is not well developed, and therefore Logan (1960) speaks of the Namib "peneplain" or "platform". Some rivers, in particular the Swakop and Kuiseb, carved valleys and deep canyons into the landscape during the Pleistocene (Martin, 1961). The river beds are filled with gravel and sand. Strong floods deposit fine-grained sediments on the higher terraces (Scholz, 1974). Since the Namib platform has only a small gradient, water runs off as sheet floods after one of the episodic rains. Levelling processes have led to the formation of additional peneplains out of which some isolated monadnocks (*Inselberge*) rise abruptly. Sometimes beds of magmatic Mesozoic basalts form long flat ridges (Du Toit, 1956). Weathering affected the basaltic rocks less than the softer rocks of their surroundings.

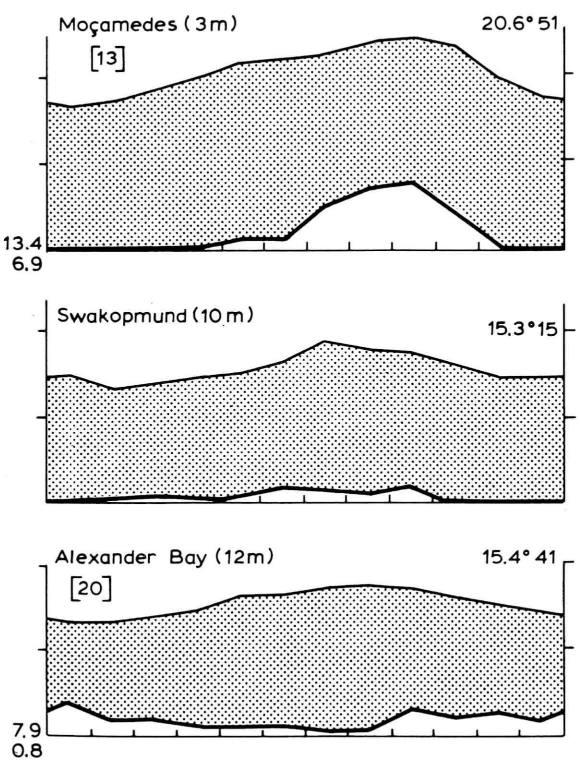


Fig. 7.7. Climate diagrams for Moçamedes (Angola), Swakopmund (Central Namib) and Alexander Bay (Southern Namib).

Large-scale *hamadas* do not occur. Sometimes small hamadas can be observed on the debris fans of basaltic monadnocks. *Serirs*, however — that is, areas where the surface is covered by rounded gravel-sized stones — are common.

The base rocks are Precambrian metamorphites such as mica schists, quartzites and marbles. The mica schists have partly been metamorphosed into granite (Martin, 1965). Mesozoic granites form some of the most important mountain complexes (Brandberg and Erongo). But, for soil formation, Tertiary crusts covering the whole area are more important.

As in all deserts, physical weathering is the most important factor in the decomposition of rocks (Rust, 1970; Besler, 1972). Because of the fogs, chemical weathering has a greater impact than in other deserts. The mostly saline fog water decomposes solid rocks especially in shady localities where the water does not evaporate too quickly. This results in the creation of holes, cavities and cavernous recesses (*Hohlkehlen*) (shade weathering: Knetsch, 1960; Besler, 1972).

Chemical transformations also take place in the soils even though they are only sporadically moist, as witnessed by the presence of clay minerals like attapulgite and halloysite (Scholz, 1963).

SOILS (by H. Scholz)

Syrozem

Syrozems ("raw mineral soils": D'Hoore, 1964) are composed of rock debris that has recently

[1]A river which carries water only episodically is in Namibia (South West Africa) called a *rivier* (plural *riviere*), a term equivalent to "wash", *arroyo secco*, *wadi* and *oued*.

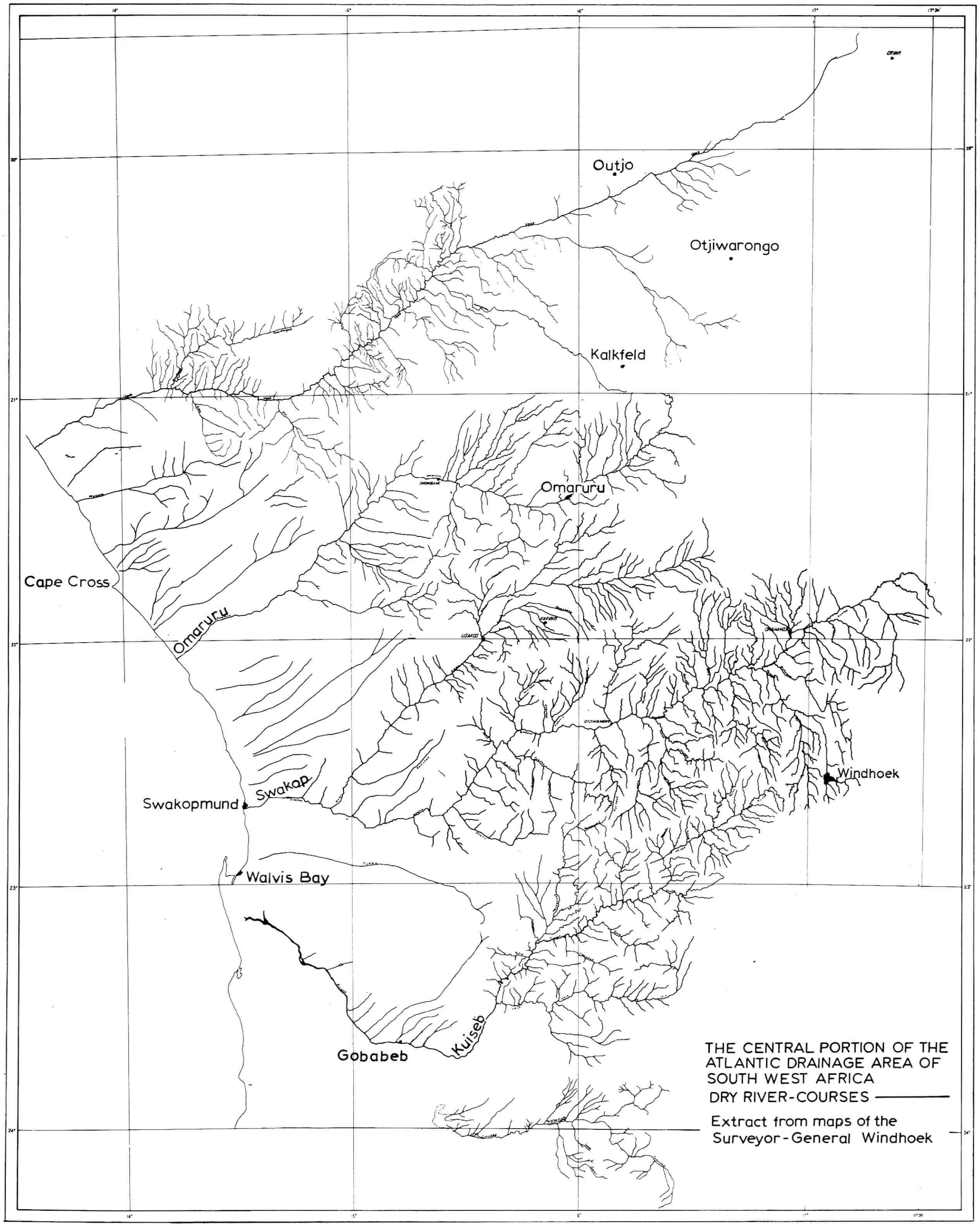


Fig. 7.8. Drainage system of the central Namib (after Stengel, 1964).

undergone physical weathering and contains very little soil. They rarely carry any vegetation, and are mainly formed on monadnocks whose rocks are exposed. The rock debris accumulates on the foot of the slopes and on the colluvial fans. Syrozems are not uniformly textured, but are composed of particles of all sizes from large gravel to fine dust, which is mostly blown in from the outside. With increasing distance from the point of origin, chemical weathering processes increase and the syrozems turn slowly into weakly developed soils (sierozems). In the Namib these are the calcareous soils and the soils with calcareous crusts.

Sands (ergs)

Ergs are found in the central Namib near the coast between Swakopmund and Walvis Bay. Because of the continuous movement of the sand, ergs have no soil and no vegetation. The extended dune area starts south of the Kuiseb. The sands of the various regions differ only in their mechanical and mineral composition. On their windward side the dune sands are composed of somewhat coarser and dark grains.

Soils with calcareous crusts

Calcareous crusts occur mainly in peneplains and on slightly eroded surfaces. In contrast to the compact crusts along the banks of rivulets and valleys, they are not always strongly cemented. They are partly underlain by marl. Various theories try to explain the formation of these crusts (Durand, 1963; Ruellan, 1967; Franz and Franz, 1968; Scholz, 1971). Apparently they are not formed under the present conditions of the Namib, since today's climate is not sufficiently humid.

Shallow, light-coloured soils have developed either on top of the crusts or between the debris particles of the weathered crusts. Their pH is about 8. They rarely contain more than 5% clay. Only loessial deposits, which occur sometimes in the soil profiles, have a clay content of up to 15%. A more or less thick layer of rock debris or gravel nearly always overlies the soil surface and protects it against erosion.

There are many transitions between soils with calcareous crusts and other soils. Only the soils of valleys and depressions need be mentioned, which are sometimes more than one metre thick. Calcareous crusts are not always present in these young soils, but they nearly always contain calcium carbonate.

The soils with calcareous crusts are found mostly in the eastern part of the central Namib. Towards the west, in the direction of the Atlantic, there is a gradual transition, first to soils with gypsum crusts containing calcium carbonate, and then to soils with salt crusts.

Soils with gypsum crusts

It is not fully understood how gypsum crusts are formed. Martin (1964) believes that the calcareous crusts once extended nearly to the coast. The yearly recurring eruptions of hydrogen sulphide gas from the mud of the sea coast provide the sulphur. It forms sulphuric acid which reacts with the carbonate of the calcareous crusts leading to the formation of gypsum. This theory seems to be corroborated by the fact that with increasing distance from the sea the gypsum content decreases (Scholz, 1963).

The soils with gypsum crusts are free of calcium carbonate. They extend up to 15 km inland, and range from shallow to medium-deep. They are covered by rather coarse debris. The light-coloured gypsum crust mostly overlies solid rock. The soil itself is yellow, light-brown, light-gray or whitish. The physical characteristics of these soils are not very different from those of the soils with calcareous crusts. If they contain any organic matter at all, it amounts to less than 0.5%.

Soils with salt crusts

These soils are very uncommon. They occur locally in small depressions without drainage. These salt crusts form at the bottom of the shallow soils. Other salt crusts develop occasionally in small valleys (*soutriviere*) where the underground water rises through the rocks and reaches the capillary region of the soil. Thus, salt swamps or *sebkhas* are formed with a rough polygonal elevated crust of saline clay.

PLANTS

General considerations

Plants as primary producers are the most important elements of all ecosystems, and plant communities form the basic units in them. In deserts with episodic and irregular rainfalls plant communities are not stable. They have to adapt themselves to the amounts of available water and therefore continuously undergo qualitative and quantitative changes. Since water is the main limiting factor and fog is more prevalent than rain in the Namib, the question arises whether there are "fog plants". These would be plants which would not need to take up water from the soil through their roots but could cover their water requirements by absorbing fog water through their above-ground parts. It is well known that the thallus of poikilohydrous lower plants (algae, fungi, lichens) takes up water from the air with a high relative humidity of more than 70%. These organisms survive periods without water in a dry anabiotic state. In the outer fog-rich Namib, such algae (*Fensteralgen*) are very common. They are known also from other arid regions (Beadle and Tchan, 1955; Vogel, 1955; Shields and Drouet, 1962). These green or blue-green algae form thin layers on the undersides of translucent stones (quartz, calcite) which lie on the soil surface. Some of these algae can also fix atmospheric nitrogen. When the stones become wet, water runs down to the underside. Protected against evaporation it persists there for some time, enabling the algae to photosynthesize. Such algae also occur on the lateral surfaces of dark stones and below weathered scales of granite, if there is enough light in these habitats. Epilithic, endolithic and humicolous (see Fig. 7.9) lichens are also common in the Namib; the saxicolous species occur on all types of stones which do not weather easily (see p. 263). *Wanderflechten* ("rolling" wind-blown lichens) also occur, accumulating in runnels (see Fig. 7.10). These lower organisms are authentic fog plants.

The normal water uptake of the homoiohydrous higher plants takes place through their roots. The cuticle covering their above-ground parts is to a limited degree permeable to water, and some plants can absorb small amounts of water through it if their tissues are not water-saturated. However, the cuticle of desert plants is very impermeable to water, and cuticular transpiration is practically non-existent. In an experiment with *Lithops* (Walter, 1973a), the "window" leaves of shrivelled plants were put in water. Their water uptake was hardly measurable. When the cuticle was injured, the plants quickly became water-saturated.

Homoiohydrous higher plants are only veritable fog plants if water uptake from the soil is not an absolute necessity for them, because they are able to absorb water easily through their shoots and do not lose this water through cuticular transpiration. Only *Tillandsia* species of the fog desert of Peru are known to behave in this way (see Walter, 1973a). Investigations with Namib species considered to be fog plants showed that they lost during the fog-less period three or four times as much water as they took up from fog. They perished without water uptake from the soil[1].

Capillary water uptake through the stomata resulting in infiltration into the leaves is also out of the question. Such infiltration of water only takes place under high pressure. The experiments of Bornmann et al. (1973) prove nothing in this respect and are ecologically meaningless.

Poikilohydrous higher plants (ferns, *Myrothamnus*) are absent from the Namib and grow only on the slopes of the escarpment and in the Karibib–Otjimbingwe area with more than 100 mm annual precipitation.

[1]Editor's note: Seely et al. (1977) and Louw and Seely (1980) reported "the use of fog at least as a supplementary source of water" (Louw and Seely, 1980) for two Namib plants. These are the only perennials of the Namib dunes, and survive for many years "with little or no rain". The succulent *Trianthema hereroensis* can take up large amounts of tritiated water sprayed on its leaves. The grass *Stipagrostis sabulicola* has an extensive superficial root system, part of which lies within the uppermost centimetre of the sand. This sand layer is often thoroughly moistened by condensed fog. When the top centimetre of sand round the plant was moistened to field capacity by tritiated water, this water was taken up by the lateral roots and appeared after 24 h in all roots, stem and leaves. When the same plants were tested seven weeks after this treatment, most of the tritium was found in photosynthates transferred to the main vertical and lateral roots. Though these plants are not "true fog plants" in the strict sense, as defined here by Walter, the authors conclude that in both species "the use of fog at least as a supplementary source of water has been demonstrated" (Louw and Seely, 1980), and that fog water is important for their survival. In this regard it is interesting that the seeds of *Stipagrostis* need at least 20 mm of rain for their germination.

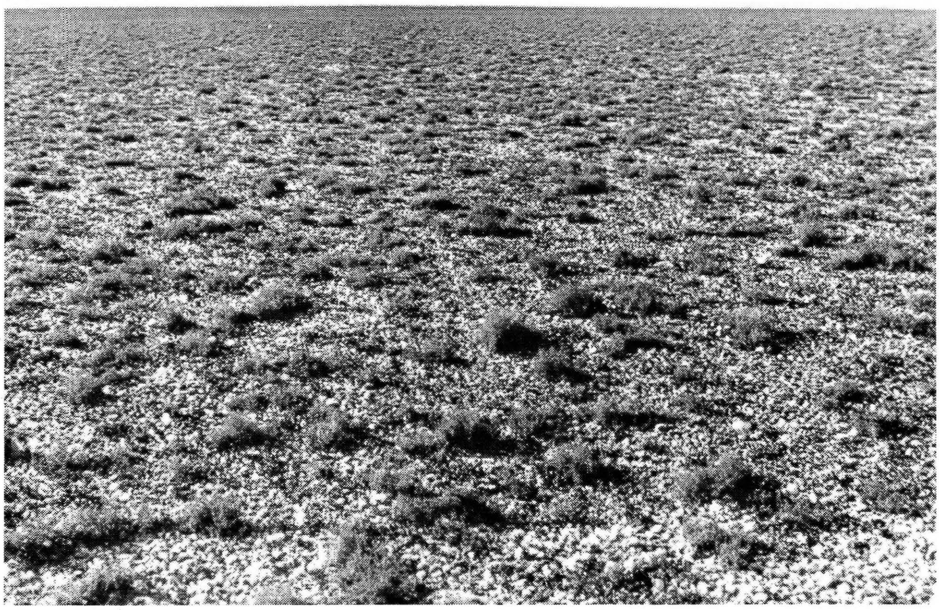


Fig. 7.9. Serir of the Namib covered by fruticose lichens (*Teloschistes capensis*, *Malme*, *Usnea* sp., *Parmelia* sp.) *c*. 40 km N of Swakopmund (photo W. Giess).

Fig. 7.10. "Rolling" black lichen [*Omphalodium convolutum* Hue = *Parmelia convoluta* (Hue) Zahlbr.] accumulated in runnels (photo W. Giess).

The fact that tamarisks (*Tamarix* spp.) under conditions of high relative humidity are covered by water drops is a purely physical phenomenon. The tamarisks excrete salt which absorbs water when the relative humidity of the air exceeds 76%. The salt solution is not taken up by the plant.

Although no fog plants are found in the Namib, fog is often of great importance for the water balance of plants because it moistens the soil and it stops transpiration temporarily.

On level surfaces fog or dew does not provide enough water for plants since the water evaporates immediately when the fog disappears. However, on rocky ground fog water runs off from a large rock surface into small rock crevices, and moistens the soil to such depths that plants rooting in these crevices are supplied with enough water. A fog condensate of 0.2 mm running off from a 10-m^2 surface supplies 2 l of water. These fog condensates are the source of water for plants growing on the monadnocks near the coast and rooting in rock crevices. They are not fog plants but "fog run-off plants".

During day-time fog, photosynthesis but no transpiration takes place even with open stomata, because there is no humidity gradient between leaf and the ambient air. With the disappearance of the fog the plants close their stomata when water stress develops, and thus prevent dangerous water loss. During fog days in Swakopmund, cut shoots of *Arthraerua* lost 6 to 10% of their fresh weight in the first two days, but in the following three days they lost no more water although the shoots remained fresh. Shoots of *Acanthosicyos* near Gobabeb behaved similarly. Therefore, plants in regions with fog can manage with much less water than plants in fog-less deserts.

It is possible that many plants of the Namib have Crassulacean acid metabolism (CAM). This is more or less certain for the many succulents, especially the Crassulaceae and the various species of *Mesembryanthemum*. Winter et al. (1978) has shown this for *Mesembryanthemum crystallinum*. This means that these plants take up carbon dioxide only at night when their stomata are open and the air in the Namib is fully saturated with water vapour, and then carry out photosynthesis during the day when the stomata are closed. Consequently, these plants could produce dry matter without substantial water loss. This would explain why in 1935 in the Namib Walter found plants of *M. cryptanthum* which had germinated after the heavy rains of 1934, and which were still growing although their roots and the basal parts of their shoots were dead. The water reserves of the older sections of the shoot were transported, without further losses, into the still-growing terminal parts (Walter, 1936).

However, as far as homoiohydrous plants are concerned, minimal amounts of water must always be available in those soil layers in which their roots grow. The roots do not have to reach the ground water table. They can use the amount of "available" water contained in humid soil layers. Since most Namib soils are composed of coarse particles, the wilting point is usually below 1% and most of the soil water is therefore available. The upper soil layers dry out quickly by evaporation after the soil has been deeply wetted. Since the capillary forces in coarse-textured soils are small, water in deeper soil layers remains there for long periods if it is not taken up by plants. Water accumulated in these layers after rain or run-off provides plants with a water source for many years, until the occurrence of another rainy year, since the perennial plants with deep roots are widely spaced and have a small transpiring surface. This is true only under the following conditions:

(1) The soil must have a certain water-holding capacity. This is the case with fine and coarse sands if they are deep enough or fill deep crevices.

(2) Water must be able to infiltrate the soil. Stone pavements and dense crusts prevent this.

(3) Water must penetrate the soil to a depth from which it cannot be lost by evaporation. With meagre rainfall this happens only in habitats where run-off from larger surfaces collects.

There are no real sheet floods. All surfaces are slightly uneven, and run-off collects first in small runnels and then in larger rivulets which unite to *riviere*. The run-off water accumulates in depressions or disappears in sand. The amount of infiltrating water and the depth of penetration increase in general in the direction of the run-off flow if the conditions mentioned under (1) are fulfilled. Accordingly, the contracted vegetation increases in the same direction.

If, after meagre rains, a small amount of run-off is formed, only the uppermost soil layers are wetted. An ephemeral vegetation develops, which consists in the outer Namib of annual species of *Stipagrostis*, and in more saline habitats of *Zygophyllum simplex*. However, even this ephemeral vegetation is unevenly distributed. It is spotty and thrives in small runnels and depressions where run-off accumulates. Wherever light local thunderstorms occur in the Namib, such green spots on which wild animals feed can be found. These local showers are not registered by the few meteorological stations, and are more frequent than one imagines.

Habitats where available water is present for prolonged periods are indicated by the presence of perennial woody species.

The vegetation of a desert with episodic rainfall is very different in years with ample rainfall and in drought years, especially when the drought has persisted for many years. In 1935, after the unusually heavy rains of 1934, the ephemeral vegetation of the Namib was luxuriant and the abundance of species phenomenal. During our later visits (H. and E. Walter in 1938, 1953, 1963 and 1975) we were much impressed by the progressive deterioration of the vegetation. A similar outburst of ephemeral vegetation occurred in 1976 after heavy rains in January to March (100 mm at Gobabeb).

The plants best suited to characterize desert ecosystems are the long-living species. They probably reach an age of many decades and can even be more than a hundred years old. The perennial plants of a given stand apparently belong to a limited number of age groups — that is, groups of plants which germinated in the same rainy year. Tree-ring analysis of suitable perennials of the Namib, in order to determine their ages, has unfortunately not been done.

The habitus and living phytomass of these perennials changes drastically, because one of the most important adaptations of desert plants to water stress consists of shedding the greatest part of their shoots. Often only one small basal shoot remains alive. This suffices for the survival of the plant, because it quickly recovers after one good rainy year. The plants thus hold out at the lower limit of existence by adapting their transpiring surface to the chance amount of available water.

An important point concerns the water supply per unit leaf surface. Walter (1939, 1973a) has shown, for the inner Namib and neighbouring areas of Namibia (100–500 mm annual rainfall), that the relation between the amount of average annual precipitation and leaf area index (LAI) is a linear function. Therefore, the water supply per unit leaf surface in arid zones is not less than that in humid regions. This is apparently also true for extreme deserts (rainfall < 100 mm) where the vegetation is not diffuse but contracted and where the latter receives additional run-off (Walter and Stadelmann, 1974). This supposition was confirmed by Batanouny (1963) and Abd el Rahman and Batanouny (1965) for Wadi Hof (Egypt).

Naturally this does not mean that plants in arid zones do not need special mechanisms adapting them to the water conditions of their habitat, like root systems exploiting a very large soil volume for water, extreme reduction of their transpiring surface, drought resistance, etc.

Succulents constitute a special case. Their developed root system takes up relatively large amounts of water after a rain, and the water is stored and used sparingly during the dry period. The Namib contains many leaf succulents (*Aloe asperifolia*, *Cotyledon orbiculata*), stem succulents (*Euphorbia virosa*, *Hoodia* and *Trichocaulon* spp.) and leaf and stem succulents (*Aloe dichotoma*). The osmotic potential of the cell sap of these species is always very high (-5 to -9 bar). The fine roots die during the dry season and develop anew after a rain. It may be assumed that all these species are CAM plants. Because of their well-developed cuticle (Zemke, 1939) their cuticular transpiration is extremely low.

The extremely succulent Aizoaceae, like *Aizoon*, *Aizoanthemum*, *Drosanthemum*, *Hereroa*, *Lithops* and *Ruschia*, differ from the above-mentioned succulents in their low osmotic potential (*c.* -20 to -50 bar) and the high chloride percentage of their cell sap (*c.* 20 to 80%). They represent therefore a transition to the succulent halophytes, but in contrast to them grow well on salt-free soils. Their cuticle is mostly very thin but extremely impermeable to water (Zemke, 1939). Their stored water suffices for more than one year.

In the Namib the stenohydrous xerophytes are an important ecological group. They survive protracted droughts by shedding their transpiring organs and by reducing their gas exchange to a minimum. Their water reserves, in contrast to the succulents, are very limited. Their osmotic potentials remain high. Plants in the Namib belonging to this group include *Adenia pechuellii*, *Kleinia longiflora*, *Pelargonium otaviense* (only short-lived leaves) and *Sarcocaulon mossamedense*.

There is only one, but very extraordinary, sclerophyllous xerophyte in the Namib: *Welwitschia*.

True halophytes and non-halophilous xerophytes of deserts are ecologically very different. In the outer Namib with its saline soils, the main phytomass is formed by halophytes. Some (*Arthraerua*, *Psilocaulon*, *Salsola* spp., *Zygophyllum*) form dune hillocks (*nebkas*; see Fig. 7.11). These plants do not develop adventive roots in the dry dune sand. The main root reaches the soil below the sand and there gives rise to vertical and horizontal branches. Some of the vertical branch roots reach the wet soil layers. The osmotic potential of the cell sap of these species is relatively low (Table 7.8). They differ in their chloride content. The non-succulent sclerophyllous *Arthraerua* with reduced scale-leaves contains little chloride but much soluble sulphate. The sulphate content (expressed as percentage of the chloride) of the extreme succulents of the Namib is 0.0 to 2.8%, in the *Zygophyllum* species with succulent leaves it is 5 to 8.5%, and in *Arthraerua* it is 18.5 to 62.5%. There seems to be an interesting relationship between sulphate content and scleromorphy, because chlorides increase the degree of succulence and the hydration of proteins, but sulphates cause dehydration. The same is true for the chloride-excreting *Tamarix*, which has a high sulphate content. *Arthraerua* and *Tamarix* are sulphate halophytes in contrast to the chloride halophytes. Both types can grow next to each other on the same soil.

Alkali halophytes (always Chenopodiaceae), which are common in Central Asia and Utah, are absent from the Namib.

TABLE 7.8

Osmotic potentials and chloride content in % of the osmotic potential of four hillock-forming halophytes

Species	Osmotic potential (bar)	Chlorides (%)
Zygophyllum stapfii	−27.5 to −55.6[1]	22.1–39.5
Zygophyllum simplex	−16.3 to −53.2	10.8–43.7
Arthraerua leubnitziae	−23.4 to −40.4[2]	2.8–15.6
Psilocaulon salicornioides	−28.6 to −31.1	9.1–12.4

[1]In 1932 before the rains, values of −51.5; [2]in 1932 before the rains, values of −56.2 (after Boss, 1941).

Main vegetation types and their distribution in relation to climate and soil[1]

An outline of the vegetation of the Namib has recently been given by Giess (1981), including records of seventy vegetation stands and a list of species by families.

In view of their instability it is difficult to define ecosystems of the Namib according to the dominant plant associations. It is more useful to clarify the ecosystems, at least partly, according to predominant geomorphological features, which in deserts are more characteristic than the vegetation.

The following biotopes may be distinguished:

Outer Namib: (1) the peneplains; (2) monadnocks and rocky ridges; (3) rivulets and smaller riviere; (4) the oases of the large "alien" riviere (*Fremdling Riviere*) (Kuiseb, Swakop with Khan); (5) dunes without vegetation but with fauna.

Inner Namib: (6) large grasslands; (7) the *Welwitschia* biotope of the transition zone; (8) monadnocks and riviere; (9) pre-Namib (*Vornamib*) along the escarpment.

Vegetation of the peneplains

These areas constitute the largest part of the platform of the outer Namib, which rises with a constant slope from sea level in the west to 1000 m at the foot of the escarpment. The surface is covered by a desert pavement consisting mainly of pebbles and stones of light-coloured quartz, occupying from 10 to 50% of the surface. Fine sand, which in many cases is cemented into lumps (often by gypsum), lies below the pavement.

Lichens growing on the stones and "window" algae below translucent stones are the only permanent vegetation.

The lichens of the outer Namib are an important component of the vegetation. They gradually disappear as one moves inland and the frequency of fogs decreases, and are completely absent from the inner Namib. Doidge (1946) cited 24 species from the rocky coast of Lüderitz Bay and only a few from the central Namib. Mattick (1970), who described the lichen vegetation between Swakop-

[1]Lichens collected by E. Walter.

mund and Cape Cross, mentioned well-defined stands of the dark orange fruticose lichen *Teloschistes capensis*, which grows on the soil in the form of cushions and covers up to 40 to 60% of the soil. These stands extend over several kilometres (Fig. 7.9). *Ramalina maculata* var. *tenuis* and the small foliose, nearly black, *Xanthoparmelia hyporhytida* are interspersed. Another lichen stand contains the dark foliose *Omphalodium hottentottum*. The "rolling" lichen *Omphalodium convolutum* is also present. When dry, this lichen is rolled up into dark tubes. The sand blows them together and it can be found in large masses in small depressions and runnels, as for instance along the road from Swakopmund to Khomas at a distance of 15 to 25 km from the sea (Fig. 7.10).

Crustose lichens grow on stones of the desert pavement and on the monadnocks near the coast. On black dolerite rocks north of Swakopmund the orange *Caloplaca indurata* (det. V. Wirth) occurs as well, as two other sterile *Caloplaca* species, the very small *C. elegantissima* and *C. diploplaca* var. *gracilior* on quartzite stones of the pavement, and the crustose *Parmelia namaensis*.

East of Walvis Bay the foliose lichen *Omphalodium hottentottum* covers the rocky slope of the Swartbank Mountains together with *Caloplaca indurata*. On soils with a gypseous crust grow the greyish crustose lichens *Caloplaca volkii* and *Lecidella crystallina* (det. V. Wirth). The last was also found on marble stones. On the coast near Cape Cross, Walvis Bay and Lüderitz Bay occur bushels of *Combea mollusca*, a whitish coral-like lichen with dark apothecia.

Lichens near the coast often grow on the lee side or in crevices of the rocks where they are protected against sand blasting, and then do not thrive on the rock surfaces facing the sea, exposed to salt spray. They are also, as a rule, not found on woody plants like *Arthraerua leubnitziae*; but a very old *Acacia giraffae* at the rocky foot of the Swartbank Mountains was covered by *Ramalina pollinaris*, another *Ramalina* species, *Usnea* cf. *hirta* and *Teloschistes chrysophthalmus*. There and on the twigs of old *Lycium* shrubs in the lower part of the Swakop riviere, the yellow *Xanthoria flammea* or *Teloschistes chrysocarpus* were found. A green foliose *Parmelia* species occurred on stones in the Swakop Valley. Commonly this lichen is found on stones of the escarpment and the highlands. On the way to and around Gobabeb near the Kuiseb, small yellowish thallus chains of *Acarospora immixta* grow on granite stones. Otherwise the plain surfaces are completely devoid of vegetation except in years with a very good rainfall. In 1935, after the heavy rains of 1934 (p. 261), the ground was mostly covered with very succulent herbaceous species of Aizoaceae (from 20 to 50% cover, according to topography), wherever the sand layers were thick enough. The plants had feebly developed roots, but in 1934 stored sufficient quantities of water in their leaves and succulent shoots to continue growing for more than a year. In 1935 they had already started to die off in the more elevated areas, or were already completely dry and dead. In 1936 all had died including those in the lower-lying regions (G. Boss, pers. comm., 1937). In 1935 the dominant species were: *Mesembryanthemum cryptanthum*[1], *Drosanthemum luederitzii*, *Aizoon dinteri*, *Zygophyllum simplex*, seedlings of the perennial *Psilocaulon salicornioides* (Fig. 7.11), *Tetragonia reduplicata*, *Zygophyllum stapffii* and the non-succulent *Arthraerua leubnitziae*. The perennial species have taproots, and persist near the coast only in slightly depressed floodplains of the Namib riviere which are without desert pavement and where the soil is deeply wetted. These plants form sand hillocks up to 1 m high (nebkas).

The nebkas constitute a characteristic feature of the outer Namib since they are the only vegetation after many rainless years. The dominant hillock-forming species are the halophytic species *Arthraerua*, *Salsola* and *Zygophyllum stapffii*. The salt content of the soil apparently decreases from *Salsola* to *Zygophyllum*. Nebkas formed by *Psilocaulon* and *Zygophyllum clavatum* are found north of Swakopmund on the sea coast just above the high water line. In 1935 luxuriant plants of *Mesembryanthemum guericheanum* grew between the nebkas. In later years these plants were found only sporadically on humid rivier surfaces.

Vegetation of monadnocks and rocky ridges

In arid areas, crevices and accumulations of sand and debris below rock surfaces, which are relatively humid, are favourable ecological niches. Ridges of quartzite, dolerite and marble are biotopes preferred by succulents. The following small

[1]Nomenclature after Merxmüller (1972).

Fig. 7.11. "Nebkas" formed by *Psilocaulon salicornioides* near the high water line, where ground water seeps into the sea; 60 km N of Swakopmund (photo W. Giess).

Fig. 7.12. *Trichocaulon pedicellatum* growing in niches of crystalline marble near Walvis Bay receiving only water condensed from fog infiltrating into the rock fissures (photo W. Giess).

succulents appear, amongst others: *Hoodia currori*, *Lithops ruschiorum*, *Trichocaulon clavatum* and *T. pedicellatum* (Fig. 7.12); also stenohydrous xerophytes (p. 261) like *Kleinia longiflora*, *Othonna protecta*, *Pelargonium otaviense*, *Sarcocaulon mossamedense*, *Adenia pechuelii* with a tuberous stem, and larger succulents like *Cotyledon orbiculata*, the prostrate *Aloe asperifolia*, *Euphorbia gariepina*, *E. lignosa*, and the large candelabrum *Euphorbia* species, *E. virosa*. The halophilous *Arthraerua*, *Salsola*, *Sesuvium sesuvioides* and *Zygophyllum stapffii* appear sporadically. After a rain various herbaceous species are also found, like *Acanthopsis*, *Blepharis*, *Gazania jurineifolia*, *Helichrysum roseoniveum*, *Monechma arenicola*, *Petalidium* and *Sutera maxii*. In the rivulets which unite to form small riviere, species are found which will be mentioned in the next section. Since granitic mountains weather by exfoliation, they are mostly devoid of vegetation, but run-off collecting at their base and wetting the soil deeply permits the presence even of plants requiring relatively a lot of water.

Vegetation of the Namib riviere

Many small erosion runnels and rivulets on the large plain meet and form deeper and wider riviere with sandy bottoms which either are branches of the large "alien" riviere or disappear without reaching the sea. The map of Stengel (Fig. 7.8) shows how many riviere dissect the Namib. The largest rivier of the Namib is the Tubas Rivier. Seepage from this rivier is probably the water source for the *Salsola* hillocks along the road from Swakopmund to Walvis Bay. Many riviere between the Swakop and Omaruru riviere disappear in the slight depressions of the wide floodplains, which are covered by dune hillocks formed by *Arthraerua* or *Zygophyllum stapffii*. Ground water flowing towards the sea seeps down on the shore near the high water line and apparently permits the growth there of *Psilocaulon* and *Zygophyllum clavatum* (see above).

The riviere carry water only rarely, after a heavy rain. The water seeps into the sand of the rivier bottom and either forms a ground-water table there or flows slowly down the rivier below ground.

Quantitatively the water supply of the rivier plants improves down-river, but qualitatively it often deteriorates as the salt content of the water increases, either due to evaporation or by salt import from branch riviere. The vegetation changes accordingly.

Typical plants are *Adenolobus pechuelii*, *Asclepias buchenaviana*, *Citrullus ecirrhosus*, *Commiphora saxicola*, *Gomphocarpus fruticosus*, *Parkinsonia africana*, *Sesbania bispinosa* and small bushes of *Acacia reficiens*. There are in addition many herbs which have a wide distribution further to the east. In this area they are restricted to the most humid biotopes, and germinate profusely after the rivier has been flooded.

Plants of the brackish riviere are *Aizoon dinteri*, *Heliotropium curassavicum*, *Sesuvium sesuvioides*, *Zygophyllum simplex* (herbs), *Arthraerua leubnitziae*, *Zygophyllum stapffii* (woody perennials) and *Tamarix usneoides* (small trees).

Vegetation of the large "alien" riviere

The "alien" riviere originate in the rainy high plateau. Whenever it has rained there, these riviere flow and carry water to the sea even when no rain has fallen in the Namib. Sometimes the water seeps into the sand of the rivier bottom and does not reach the sea. Fig. 7.13 shows how much water reached the Atlantic through the Swakop Rivier from 1893 to 1963. Much ground water accumulates in the deep loose sediments of the rivier bottom. With a slope of 1:100 it flows below ground and reaches the surface only where a rocky ridge forms a dam in the rivier. Even when the ground water stops flowing some ground-water "lakes" remain, transforming each "alien" rivier into a string of oases. In the last century these oases formed the avenue of commercial ingress by ox wagons from Sandwich Harbour and Walvis Bay inland (Vedder, 1973).

Each flood destroys the vegetation in the rivier bottom. Vegetation remains only on the banks and the higher terraces. Because of the ample water supply luxuriant gallery forests develop there. The vegetation of the highland plateau is being progressively destroyed by over-grazing causing more run-off and larger floods in the riviere. Consequently, the peak floods of the Swakop during the last decades have become torrential and dangerous, eradicating more and more trees (Seydel, 1951). On the Kuiseb however magnificent forests can still be found.

The most important trees (often 12–20 m high) are: *Acacia albida* (Fig. 7.14), *A. giraffae* (*A. crio-*

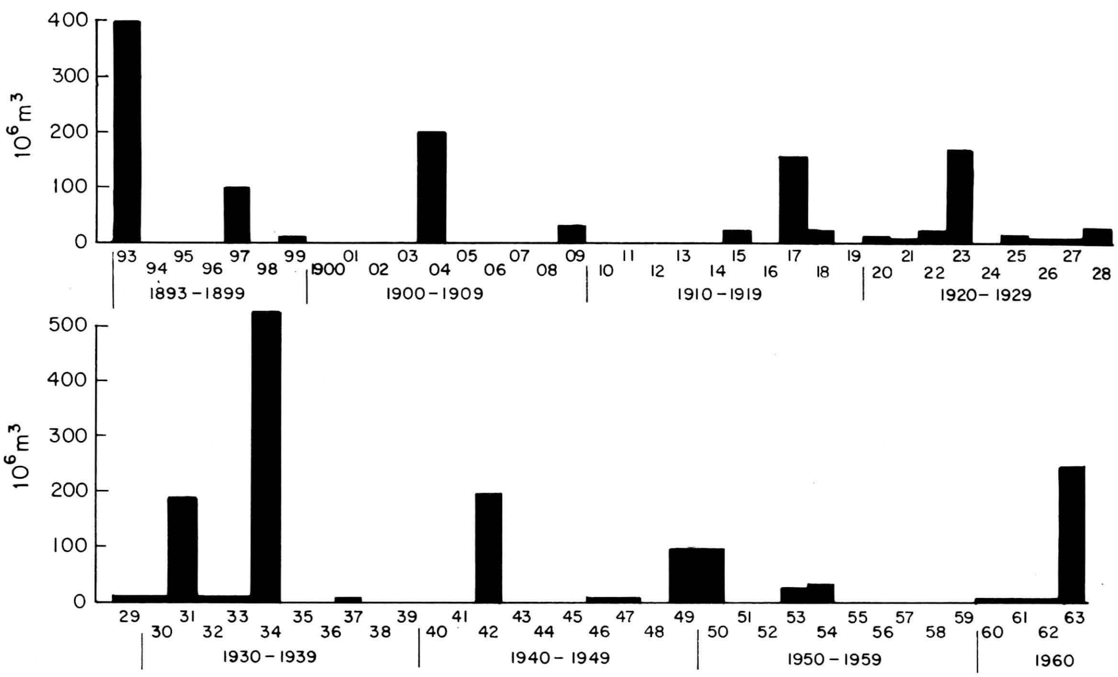


Fig. 7.13. Discharge and estimated run-off amounts carried by the Swakop Rivier (1893–1963) into the Atlantic (after Stengel, 1964).

Fig. 7.14. Dense stand of *Acacia albida* on a terrace of the Kuiseb (in background). In foreground *Eragrostis spinosa* and right of it *Nicotiana glauca* (an American neophyte) growing in the sandy rivier bed. They are carried away by each flood. (Photo W. Giess.)

loba), *Azima spinosissima*, *Euclea pseudebenus*, *Lycium tetrandrum*, *Salvadora persica*, *Ziziphus mucronata* and *Tamarix usneoides* (on saline soil). *Lycium* and *Tamarix* collect sand and form dune hillocks. *Ricinus communis* and *Nicotiana glauca* (an immigrant from the New World) develop into small trees. Between floods the following plants are found on sand fields: *Argemone mexicana*, *Codon royeni*, *Datura innoxia*, *Psoralea obtusifolia* and *Tribulus zeiheri*, with many grasses, especially *Stipagrostis namaquensis* ("rivier grass") and the woody *Eragrostis spinosa* (Fig. 7.14). These two latter species form dune hillocks up to 2 m high.

In addition, many species from the inner Namib grow in these oases, as do species typical of saline soils. The ground water of Kuiseb is practically non-saline, but that of the Swakop and its side rivier Khan contain salt. The soils of the outer Namib are always somewhat saline. The strong surf of the Atlantic sprays small droplets of sea water on the coast and a mixture of salt spray and fog is blown inland. It can be calculated that several grams of salt, perhaps up to 20 g, are deposited in this way on 1 m^2 of soil annually (Walter, 1936; Boss, 1941). After a rain the many side riviere carry this salt into the Khan and the Swakop. Wherever the ground-water table is near the surface evaporation is very high, and consequently the water is very saline. Sometimes salt crusts form on the surface, while the water in deeper soil layers contains little salt. Therefore, halophilous and non-halophilous species can grow in the riviere next to each other. This is the case in the Swakop forests where the halophilous *Tamarix* grows together with non-halophilous trees (see p. 262). The following plants are found in highly saline habitats: *Arthrocnemum affine*, *Atriplex vestita*, *Heliotropium curassavicum*, *Juncus arabicus*, *Mesembryanthemum guericheanum*, *Odyssea paucinervis*, *Psilocaulon salicornioides*, *Suaeda plumosa*, *Zygophyllum simplex* and above all *Tamarix*. On the estuary of the Swakop extensive stands of halophytes are found wherever the ground-water table is high and salt accumulates on the soil surface.

On the lower Kuiseb, however, many fresh-water swamps occur. The estuary of the Kuiseb is blocked by sand dunes which dam the ground water. The water does not become saline by evaporation because it flows through the sand into the sea. Partly it seeps through the dunes in a southerly direction and emerges as a fresh-water source near Sandwich Harbour where it also forms a swamp. The swamp plants include *Cyperus marginatus*, *Juncellus laevigatus*, *Phragmites australis*, *Scirpus dioicus* and *Typha latifolia* ssp. *capensis*. The ground water of the Kuiseb is used as drinking water for Walvis Bay and Swakopmund. The demand for drinking water is continuously increasing. A large water pipeline is now being built leading to the uranium mine near Rössing. Since the ground-water supply of the Kuiseb estuary is limited, the ground-water table may be dangerously lowered. The swamp plants have already been damaged by drought. Between Walvis Bay and Gobabeb, for instance, all the tamarisks of a wide flat are already completely dead.

The dunes

South of the lower Kuiseb lies a large dune area. It is from 30 to 130 km wide and stretches without interruption to Lüderitz Bay. The sand overlies the Namib platform. Only a few monadnocks project from it. The dunes, 240 m high, are probably the highest of the globe. The dune area is composed of chains and fields of typical barkhans. The sand is yellow-brown near the coast and brilliantly red inland.

No ground water accumulates in the moving sands, which are only superficially moistened by fog. The dunes therefore carry no macro-vegetation, but micro-organisms and a rich fauna are present.

On the edges of the dune region only three plants occur: *Acanthosicyos horrida* (Fig. 7.15), *Eragrostis spinosa* and *Stipagrostis sabulicola*. These plants apparently germinate on the wet sand after a heavy rain and reach ground water with their roots. Their shoots are constantly being covered by sand and growing back out, thus forming nebkas. On the more stable sandy surfaces of the interdune valleys an ephemeral vegetation (mainly *Stipagrostis* and *Trianthema*; see p. 258) develops after heavy rains (e.g. in 1976).

The large grasslands of the inner Namib

The ecological conditions of the inner Namib are less complex than those of the outer Namib. Fog is not important. The vegetation is dependent on summer rains which are so irregular that farming

Fig. 7.15. *Acanthosicyos horrida* growing on sand dunes of the lower Kuiseb. Its spiny fruits are an important food for the Topnaar Hottentots. (photo W. Giess.)

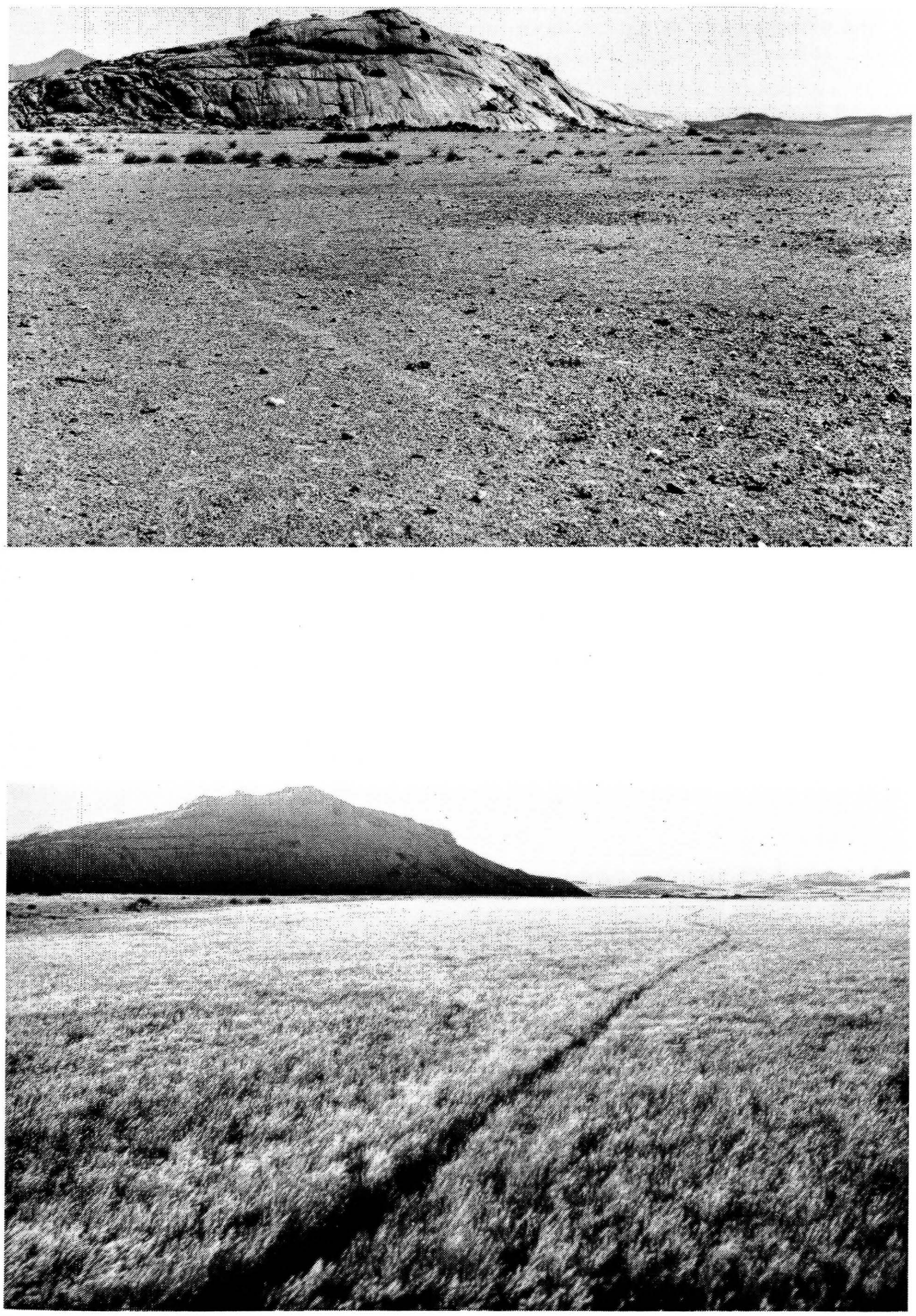
has been given up. The region from the Khan to the Kuiseb is today a wild game reserve. The inner Namib is covered by sandy debris overlying the rocks of the platform. Summer rains are stored in the debris enabling the formation of a grass cover (Fig. 7.16). Wherever the ground is stony, as for example between Usakos and Swakopmund, the grassland is replaced by a zone of *Euphorbia gregaria*. A similar vegetation occurs in the southern region of Namibia (in the area of Bethanie) where the canyon of the Fish River has been carved into the high plateau.

Further west, where it is drier, *Euphorbia* is restricted to rivulets, and *Aloe asperifolia* appears on the plains, growing in "fairy rings". The tips of its low stems point north. Still further to the west, the gravel desert of the outer Namib is without any vegetation.

All the grasses of the inner Namib belong to the genus *Stipagrostis*. *S. obtusa* (Fig. 7.16B), the smallest perennial species, has the lowest water requirement, *S. ciliata* a larger requirement and *S. hochstetterana* and *S. uniplumis* the largest requirement. These species replace one another in the above sequence from west to east, with mixed stands between the pure ones. The grass cover completely consumes the available water. Cover and biomass vary greatly between years and sites depending on rainfall (see below). The moist upper soil horizon is completely filled with the roots of these grasses, leaving no room for herbs or woody plants. When the water is used up, the grassland becomes yellow. The meristems of the shoot apices remain alive enveloped by their dry sheaths. The roots are protected against the dry soil by their dead rhizodermis, covered by the dead root hairs and adhering sand particles. Together they loosely envelop the living vascular cylinder (Henrici, 1929; Walter, 1939). After the first rain, the dead root envelope absorbs water and new root hairs are formed. It is not known if the grasses can survive a number of drought years in this semi-dormant condition.

The *Welwitschia* biotope of the transition zone

By far the largest number of *Welwitschia* plants (5000–6000 according to an estimate by Giess, 1969) grow in the transition zone between the outer and inner Namib about 50 to 60 km from the coast in a triangle formed by the Khan and the Swakop. Their habitat in this region is not the plain but a wide, slightly depressed, sandy-gravelly rivier. It



A

B

Fig. 7.16. Area at the foot of a gigantic monadnock (*Blutkuppe*) *c.* 100 km inland from the sea coast. A. Before the rain. B. After the rain covered by *Stipagrostis obtusa.*

slopes down towards the south and there becomes a typical deep side rivier of the Swakop. The broad rivier has steep banks, about 1 m high. This indicates that after a rain the rivier flows at its full breadth, but with a slow current. At a depth of from 80 to 150 cm the rivier bottom is composed of a hard crust cemented by carbonate. In 1935 the water content of the soil was 2.3% at a depth of

40 cm, and 5.9% at 60 cm, the wilting point being below 1%. One plant excavated by Giess had a well-developed root system. Its taproot reached the hard crust and the fine roots penetrated the crust which contains capillary water. The branch roots were at least 1.2 m long. Some of the *Welwitschia* plants grow on the upper rim of the rivier. It may be assumed that their roots reach the humid soil of the rivier.

In 1935, after the rains of the preceding year, the habitat of *Welwitschia* still contained considerable available soil water. Besides *Welwitschia*, a few individuals of *Celosia*, *Cleome*, *Sesuvium* and *Sporobolus* also grew there. However, in 1975 only *Welwitschia* had survived.

On the southern shore of the Swakop in 1935 *Welwitschia* grew together with *Arthraerua*, *Chascanum garipense*, *Sesuvium* and *Zygophyllum stapffii* on a plain which turns into a rivier with *Adenolobus*, *Parkinsonia* and *Salvadora*. The same is true for its habitat near the Hope mine. The rivier there is 100 to 150 m wide and 3 to 5 m deep. Nearly all of the many *Welwitschia* plants grew in the main rivier or in the many secondary riviere or rivulets. Bushes of *Acacia*, *Adenolobus*, and well-developed plants of *Zygophyllum stapffii* indicate here too the presence of available water and the absence of torrential floods.

The southernmost population of *Welwitschia* occurs on a northern secondary rivier of the Kuiseb, 0.5 km distant from the main rivier and 1.5 km west of Homeb (Fig. 7.17). About 60 km from the coast, the plants again grow in a sandy slightly sloping rivier. At 25 km from the coast only sporadic individuals are found, as for instance in ravines in rocky slopes of secondary riviere of the Swakop near Palmhorst.

In summary, it may be stated that the plant in the southern and driest region of its distributional range grows with few exceptions in habitats where a minimum of soil water is always available. This water is supplied by floods. The roots do not reach the ground-water table as has often been supposed. *Welwitschia* apparently avoids riviere with stronger flood currents, probably because its seedlings cannot survive when covered by sand. The water supply from the soil is limited but suffices to guarantee the survival of this non-demanding plant (Walter and Breckle, 1984).

The overall distribution of *Welwitschia* and nearly all its biotopes have been described by Kers (1967; see also Giess, 1969; Walter, 1973a). Only in

Fig. 7.17. *Welwitschia mirabilis* growing on its southernmost habitat in a secondary rivier of the Kuiseb (photo W. Giess).

climatically more humid regions does the plant occur on plains or slopes. In the drier parts of its distributional area *Welwitschia* grows in biotopes with flood-water supply. The description given by Kers (1967) of its various habitats confirms this statement.

Fog is not a water source for *Welwitschia*, though it has sometimes been thought to be so. This is because moving fogs rarely reach the inner Namib, and because the leaves of *Welwitschia* lie close to the soil and are hardly able to condense fog. Furthermore, the scleromorphic bilateral leaves possess no structures enabling them to absorb water. The cuticle is very thick, and stomata and stomatal apertures are strongly cutinized (Sykes, 1911; Takeda, 1913; Walter, 1936; Zemke, 1939; Walter and Breckle, 1984).

The leaves cannot be wetted by water. Water vapour uptake from fog would be possible by water vapour diffusion through open stomata. The osmotic potential of leaf cells was found to be −35 bar, corresponding to a relative humidity of 97.5%. At zero turgor then the corresponding relative humidity of the leaves is 2.5% below that of saturated air. A minimal uptake of water vapour can therefore not be completely excluded, but it would hardly play an important role in the overall annual water balance of the plant.

It may be assumed that the rates of photosynthesis and transpiration of *Welwitschia* are high when the stomata are open and the water supply is ample, as is the case with all sclerophyllous plants. Through closure of stomata transpiration can be minimized. Recent experiments indicate that removal of the cuticle has no major effect on transpiration (Bornmann et al., 1974). During protracted droughts the leaves dry and die down to their basal meristems, reducing the transpiring surface to near zero. After a rain the meristems quickly produce new leaf tissue. In this way the plant adapts itself to the prevailing conditions.

Few young plants are found in stands of *Welwitschia*. Apparently germination and survival of seedlings takes place only in exceptionally favourable years. An observation of Bornmann et al. (1972) is of interest in this respect. They report that the production of viable seeds is strongly reduced because *Aspergillus niger*[1] infects the punctures made in the seeds by the ever-present bug *Probergrothus sexpunctatis*.

As so far known, *Welwitschia* is the only gymnosperm species which has the enzyme system necessary for crassulacean acid metabolism (CAM) (Dittrich and Huber, 1974), and contains the peripheral reticulum in the chloroplasts of its bundle sheaths which is typical for CAM and C_4 plants (Whatley, 1975). Its typical δ^{13} C values[2] are shown in Table 7.9.

However, newer experiments under natural conditions in the Namib Desert have shown that *Welwitschia* has a normal C_3 photosynthesis. There is no uptake of carbon dioxide during the night by its sclerophyllous leaves (Von Willert et al., 1982; Walter and Breckle, 1984).

[1]This fungus, known also as *A. welwitschiae*, forms conidia, indicating a relative humidity (hydrature) of over 80% (Walter and Kreeb, 1970).

[2]Smith and Epstein (1971) defined $\delta^{13}C$ (in ‰) as:

$$\text{“}\left[\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1\right] \times 1000$$

where R = mass 45/mass 44 of sample or standard CO_2. The standard is carbonate from the fossil skeleton of *Belemnitella americana* from the Peedee formation of South Carolina (PDB_1).”

TABLE 7.9

$\delta^{13}C$ values[1] of *Welwitschia mirabilis* at different distances from the coast (after Schulze et al., 1976)

Distance from the coast (km):	16–19	45–62	69–75	130–142
Vegetation type	lichen desert	grassland	grassland	savanna
$\delta^{13}C$ values (‰)	−19.63	−21.60	−22.18	−21.64

[1]Typical C_3 plants have $\delta^{13}C$ values of *c.* −25‰, C_4 plants of *c.* −12‰. The values of CAM plants lie between those of C_3 and C_4 plants.

Vegetation of monadnocks and riviere of the inner Namib

The precipitation in these areas is higher than in the outer Namib. Therefore, the flora and vegetation are richer in spite of the less frequent fogs (121 species of angiosperms in the granite mountains of Mirabib, 35 km east of Gobabeb). Commonly found are the shrubby *Acacia giraffae*, *Boscia*, *Rhus marlothii*, species of *Commiphora*, especially *C. saxicola*, *Parkinsonia africana*, *Montinia caryophyllacea*, and *Lycium*, the dwarf shrubs *Adenolobus*, *Dyerophytum*, *Sarcocaulon* and many herbs and grasses like *Stipagrostis ciliata*, *S. hochstetterana* and the large succulent *Euphorbia virosa*.

Aloe dichotoma grows in the inner Namib on slopes of mica schist. All the riviere carry fresh water, and even in the small ones trees like *Acacia giraffae*, *Boscia* and *Commiphora pyracanthoides* grow together with many herbs and grasses which are absent from the outer Namib.

Vegetation of the pre-Namib

The Namib has no sharp boundary towards the east. The vegetation gradually becomes more luxuriant and varied as a function of the increasing precipitation. The escarpment in the region of the central Namib belongs to the pre-Namib, whereas the southern Namib extends up to the high plateau.

Low trees with thick succulent stems but normal twigs and leaves are characteristic of the pre-Namib between the Khan and Kuiseb. They shed their leaves during the dry period. Such trees are various species of *Commiphora*, *Euphorbia guerichiana*, *Moringa ovalifolia* and three species of *Cyphostemma* (Vitidaceae). Morphologically these plants resemble plants of the southern Sonoran Desert and the Brazilian caatinga.

The poikilohydrous *Myrothamnus flabellifolia* (Rosales) of the pre-Namib merits special mention. In its dry state the plant looks like a broom, with bundled twigs and brownish folded leaves. About thirty minutes after a rain twigs and leaves unfold and the small bush becomes green. When the soil dries out and there is no more available water to be taken up by the poorly developed root system, the plant returns to an anabiotic state. The physiology of this process has been summarized by Ziegler and Vieweg (1970). The species occurs in Namibia exclusively in a narrow climatic region, especially in the pre-Namib. It grows on rocky slopes of marble or mica schist. Little is known of its habitat conditions.

The highest mountain in Namibia, the Brandberg, with an estimated annual precipitation of between 100 and 200 mm (Lempp, 1956), is part of the pre-Namib. Its vegetation has been described by Nordenstam (1974).

ANIMALS

General

Animals as consumers are dependent upon primary production of plants. In deserts primary production is subject to great variations because of the unpredictable and irregular water supply. This naturally affects animal production. However, animals, in contrast to plants, have the power of locomotion. Large mammals and birds can move over large distances and change biotopes when looking for food. Others cannot, and are bound to one or two biotopes. These are therefore much more subject to the vagaries of plant production.

Kühnelt (1965, 1975) surveyed the most important consumers of the various biotopes around Gobabeb.

Ants (Myrmicinae), beetles (Tenebrionidae) and a rodent (*Gerbillus vallinus vallinus*) are consumers on the sparse vegetation of gravel desert of the outer Namib, where a gecko (*Ptenopus carpi*) lives as a predator.

On rocky ridges carrying more vegetation, Diptera, butterflies (mostly Lycaenidae), Tenebrionidae, ants, Coccidae (on *Zygophyllum*), mites (*Microcaeculus*), pseudoscorpions, geckos, and scorpions are found. The last two are predators, the scorpions being active by day and the geckos by night. The birds present are a raven (*Corvus albus*), bustard (*Lophotis*), falcon (*Melieraz musicus*), eagle owl (*Bubo africanus*) and some smaller birds. The jackal is an occasional visitor.

The animal life of the grasslands of the inner Namib is much richer. Rodents (mice), hares, Tenebrionidae, grasshoppers (Acridiidae) and the predatory centipedes (*Scolopendra*, etc.) and reptiles are present, as well as partridges, ostriches, springboks, oryx antelopes, zebras and the predatory eagle owl, falcon and jackal.

The large riviere like the Kuiseb are populated by a rich fauna. Aquatic animals live together with algae in the water holes. Plant-eating Tenebrionidae, larvae of Diptera, masses of "bombardier" beetles (*Brachinus* spp.) and predatory Histeridae are found in humid habitats. In the litter of the gallery forests live many Tenebrionidae, weevils (Bruchidae) and deathwatch beetles (Anobiidae), which consume the dry seeds of *Acacia* spp., and xylophagous beetles, which eat dry wood. Scorpions, spiders and solitary wasps occur below the bark of trees. On the soil live termites, ants and ant lions. There are many species of rodents and birds which consume plants, insects or rodents. Rodents are also the prey of the snakes *Bitis arietans* and *B. caudalis*. A rich fauna also exists on the steep shores of the riviere (granitic rocks, caves). Mice, beetles, grasshoppers, caterpillars, ants, scale insects, spiders and the Namib chamaeleon live in the nebka biotope, on the edges of dunes where *Acanthosicyos horrida* or *Stipagrostis sabulicola* grows, and on sand fields.

The fauna of the large dunes is rich in endemic species. This strange ecosystem lacks primary producers altogether. Detritus blown in from the outside constitutes the energy source of secondary producers. Kühnelt (1965) has shown that this detritus is composed of litter derived from *Stipagrostis gonatostachys* and *S. sabulicola*, together with protein-rich remains of dead animals (insects) either living in the dunes or blown into them. Wind removes this detritus continuously from the windward side of the dunes to their lee where it glides down to the dune base. It is eaten by psammophilous Tenebrionidae and to a lesser degree by termites (*Psammotermes granti*). Small predators like nocturnal Solifugae and spiders (Araneidae) are the next link in the food web. The nocturnal mole (*Eremitalpa granti namibensis*) and day-active lizards (*Aporosaurus anchietae*) are larger predators. These animals dig themselves into the sand when the sun heats the surface to a temperature above 70°C. When they are buried respiration is possible, because the sand consists of quartz grains of an average diameter of 0.5 mm and therefore about 50% of the sand volume contains air. In contrast to dune sands of other deserts these sands are dust free.

Mammals

Elephants (*Loxodonta africana*) and the black rhinoceros (*Diceros bicornis*) are today present only in the riviere of the northern Namib, but Pieter Pienaar saw them in 1793 in large numbers in the Swakop (see Vedder, 1973). They were destroyed or driven off by man. The pigmy mouse (*Mus minutioides*) living in the various biotopes of the rocky regions of the monadnocks or the canyons is probably the smallest mammal. Coetzee (1969) reported 63 species of mammals for the Namib: 1 Primates (*Papio ursinus*), 4 Insectivora, 24 Carnivora, 1 Tubulidentata, 1 Proboscidea, 2 Hyracoidea, 2 Perissodactyla, 7 Artiodactyla, 2 Lagomorpha and 21 Rodentia.

The more ambulant of these species are widely spread. These include the gemsbok (*Oryx gazella*), springbok (*Antidorcas marsupialis*), saddle-backed jackal (*Canis mesomelas*) and brown hyaena (*Hyaena brunnea*). The zebra (*Equus zebra hartmanni*) grazes on large areas but mainly on the eastern fringes of the Namib. Joubert (1971) estimated its numbers in the Namib park to be about 1000. The golden mole (*Eremitalpa granti namibensis*) however is restricted to the large region of sand dunes and to sandy rivier bottoms (Holm, 1969). The rodent *Paratomys littledalei* colonizes the coastal nebkas formed by *Salsola*, but seems also to eat *Arthraerua* and *Zygophyllum stapffii*. It is also found in lesser numbers in other biotopes. Sauer (1971) reported the occurrence of the elephant shrew (*Macroscelides proboscideus*) in various biotopes of the Tinkas plain in the east.

The colonization of the Namib by mammals took place from the east. The large riviere facilitated their migration. Coetzee (1969) stated that 63 of the 64 mammalian species found in the Namib were also present on the eastern high plateau, 49 in the pre-Namib and 40 in the riviere. None of these species lives exclusively in one of the Namib biotopes. Fig. 7.18 illustrates the relationship between the various biotopes and the number of species common to them.

Birds

The number of bird species observed in the Namib is at least twice that of the mammals, but many, as for example the vagrant birds, stay only

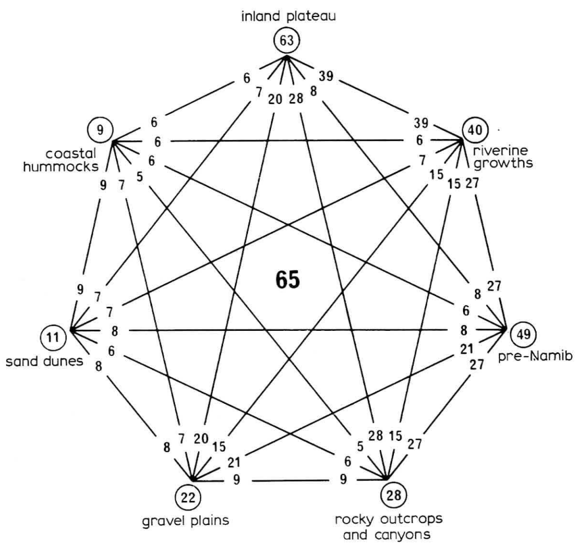


Fig. 7.18. Relationship between number of mammalian species common to different biotopes of the Namib, pre-Namib and inland plateau (after Coetzee, 1969).

temporarily in the Namib. Few birds, like the Namib lark (*Ammomanes grayi*), the desert chat (*Karrucincla schlegelii*), the pied crow (*Corvus albus*) and the rock kestrel (*Falco tinnunculus rupicola*), nest in the Namib. Most of the birds are not bound to a specific biotope. This is also true for the largest bird, the ostrich (*Struthio camelus australis*), which as a "runner" can cover a distance of over 50 km in one hour. Its ethology was studied by Sauer (1966, 1967, 1970) and its physiology by Louw et al. (1969). The ostrich regulates its body temperature (38.2–39.8°C) by rolling up its feathers, by wagging its wings and by fast panting when the temperatures are very high. A total of 66 other birds had body temperatures of 41 to 43°C (Brain and Prozesky, 1962).

Birds eating insects or juicy fruits drink rarely. Seed-eating birds do not need water when the seeds are water-soaked by dew, fog or rain. Birds visit watering places mostly in the morning and on hot days also in the afternoon (Willoughby and Cade, 1967; Prozesky, 1969). Sauer (1973) and Nel (1969) investigated vultures and owls.

Other animals

Ecological investigations of reptiles and invertebrates were made mainly near the Gobabeb station and in the large area of the moving dunes. The intense heating of the sand surfaces by insolation necessitates a regulation of the body temperatures of lizards (Brain, 1962; Hamilton, 1969). The maximum temperatures endured by nocturnal geckos (42.7–44.2°C) and diurnal lizards (44.0–45.4°C) are nearly the same. However, the geckos are most active at a temperature of 10 to 11°C, the lizards at 24 to 28°C. The lizards avoid overheating by stretching of legs, sheltering in shade and burrowing into the cooler sand layers. The lizard *Angolosaurus*, which consumes Cucurbitaceae (*Acanthosicyos*, *Citrullus*), often stays buried in sand for 20-h periods. Louw and Holm (1972) investigated the behaviour of the diurnal lizard *Aporosaurus anchietae* living in the sand dunes. It consumes insects and is eaten by the side-winding adder (*Bitis peringueyi*). This adder spends most of its time buried in sand with only its head protruding.

Koch (1962a, b) investigated the Tenebrionidae of the Namib. He subdivided the Namib into zoo-ecological regions according to the distribution of the various genera of these beetles, and his division is identical with the phyto-ecological one, because the Tenebrionidae are bound to certain biotopes. In the large dune area of the southern Namib alone twenty endemic genera were found. The ultra-psammophilous forms living in the dunes lacking any vegetation are of special interest.

Louw and Hamilton (1972) studied respiration, energy balance, nutrition and water uptake of one of these species, *Lepidochora argentogrisea*. The tenebrionid dune beetles obtain their water from fog, in several different ways. *Onymacris unguicularis* is "fog-basking" (Hamilton and Seely, 1976; Seely, 1979). The animals climb during nocturnal fogs to the crest of the dunes and take up a head-standing posture with their abdomen facing into the fog-laden wind. Fog-water collects in drops on their body and trickles down to the mouth. Three other tenebrionid beetles (*Lepidochora discoidalis*, *L. kahani*, *L. porti*) construct trenches on the sand dunes on mornings before and during advective fogs. These trenches are oriented perpendicular to fog winds and trap fog water which is taken up by the beetles (Seely and Hamilton, 1976). Water is also taken up from fog-moistened sand.

Seely (1973) also investigated the factors controlling reproduction of the Tenebrionidae.

Certain invertebrate groups in Namibia (termites, some Diptera, spiders, solifuges, scorpions, Chilopoda and Pseudoscorpionida) have been studied by Beier (1962), Lindner (1971–73), Coaton and Sheasby (1972) and Lawrence (1972, 1975). There are no domesticated animals in the Namib except for a few goats and donkeys kept by the Topnaar Hottentots on the lower Kuiseb.

SOIL MICRO-ORGANISMS

Plant or animal remains in the soil are mineralized by decomposers (fungi, bacteria). This certainly is also the case in the Namib especially where the upper soil layers contain water. The action of decomposers is even possible in the dunes because during foggy periods the sand surface is wet (Walter and Kreeb, 1970), but there are no investigations on decomposing soil micro-organisms of the Namib.

The "window" algae (p. 258) are soil micro-organisms but they are primary producers and not decomposers.

Nitrification apparently takes place in the desert soils since soil and ground water contain nitrates (Walter, 1936).

MAN

Traces of man dating back to 8000 years B.C. (perhaps to 10 000–30 000 B.C.) have been found in the Namib (Sandelowsky and Pendleton, 1970). The many endemic Tenebrionidae which are well adapted to desert conditions indicate that the climate at that time was not much different from that of today. Geologists have found evidence that there have been pluvial periods, but they apparently occurred much earlier.

Many sites of prehistoric hunters and food gatherers have been found in the Kuiseb canyon and the monadnocks. These people lived and had their fireplaces under protruding rocks and in caves near water holes. Sandelowsky showed such a location in the granitic mountains of Mirabib. She dated the remains of these different layers by the ^{14}C method at 8000, 6000 and 5000 B.C. It could not be ascertained whether these people were bushmen. Rock drawings are present (Sandelowsky, 1974).

The mountain Dama too are a very ancient people, who adopted the Nama language only at a late date and were driven into remote mountains. The Nama (Hottentots) immigrated only much later from South Africa into the central Namib. Later they came in touch with the Herero who immigrated from Botswana into the Kaokoveld and penetrated from there along the coast to the Swakop estuary.

The Saan bushmen who once wandered in the Namib in small bands have died out. The Topnaar Hottentots are the only natives living in small numbers on the lower Kuiseb as shepherds of goats and consumers of *narass*, the fruit of *Acanthosicyos horrida*. The vegetation around their settlements, which are moved from time to time, is affected by goat grazing. Otherwise the impact of man on the Namib is very small, with the exception of a few small mines, the irrigated farms in the lower Swakop and the growing towns of Walvis Bay (the main harbour of Namibia with an important fishing industry) and Swakopmund (a cool health resort with sport fishing). A uranium mine near Rössing is being developed which, like the towns, will receive its water from the Kuiseb Rivier. The Walvis Bay–Swakopmund–Usakos railway and the four highways from the coast to the high plateau are also an encroachment on the natural ecosystems of the Namib.

STRUCTURE AND FUNCTION OF THE WHOLE ECOSYSTEM

It is not easy to identify the various ecosystems of the Namib because they lack stability as a consequence of the episodic rainfall. The rich vegetation found in 1935 after the ample precipitation of 1934 was almost completely absent in 1975. It is therefore impossible to give overall figures of biomass or production. There are no such investigations and even if there were, they would be valid only for one specific year. Only the main ecosystems can be described.

Ecosystems of the peneplains of the outer Namib

These surfaces are covered by a stone pavement and lack a permanent vegetation of homoiohydrous plants. Only poikilohydrous lichens and algae are present. They are active during the

TABLE 7.10

Total phytomass of lichens from the Namib and the Negev (after Kappen, 1975)

Species	Phytomass ($g\ m^{-2}$)
NAMIB	
Teloschistes capensis	251
Ramalina maculata var. *tenuis*	1
Parmelia deserti	6
P. convoluta	9
Total	267
NEGEV	
Ramalina maciformis	70
Diploschistes calcareus	141
Total	211

greater part of the year because of their frequent hydration by fog and dew. L. Kappen carried out some preliminary measurements of lichen phytomass at Wlotzkas-Baken, 40 km north of Swakopmund, and put these data at my disposal. The phytomass (267 $g\ m^{-2}$) (Table 7.10) is quite large, especially for this otherwise quite sterile habitat. Interestingly enough, this figure is of the same order of magnitude as that of lichens in the Negev Desert of Israel (Kappen et al., 1975). The biomass production of lichens in extreme environments (hot and cold deserts with dew or fog) is therefore quite considerable. Nothing is known of biomass and primary production of homoiohydrous plants or of the secondary production and activity of micro-consumers or decomposers. After episodic rains a green sheen of annual grasses develops locally. They are eaten by wild animals, or dry out very soon and are blown away by the wind.

Ecosystems of depressions, beach ridges and nebkas

These ecosystems are restricted to the outer Namib near the coast. They occur only in habitats where, after an ample rainfall, soil water accumulates down to a certain depth. The seedlings of the perennials form taproots which grow deeper into the soil every year and never lose contact with the available water. Blown sand forms nebkas around the shoots, which grow in height together with the plants. Only the strongest plants survive. Their roots expand horizontally. *Psilocaulon* and *Zygophyllum clavatum* colonize the region subjected to salt spray near the sea shore (see Fig. 7.11). *Arthraerua*, *Salsola* or *Zygophyllum stapffii* grow at greater distances from the shore according to the salinity of the soil. In 1934 numerous succulent ephemerals appeared also, but had disappeared in 1936 because of their shallow root systems. The plants of these ecosystems can apparently reach only a certain age. When their water supply is exhausted they die, and the nebkas consequently disappear. The most important consumer is the rodent *Paratomys littledalei* (p. 273). Logan (1960) also mentioned *Gerbillus swakopensis*, lizards and scorpions. The decomposers are not known. The dead plant parts persist as litter in the dunes since the sand is dry and is wetted only superficially by the fog. Perhaps their complete decomposition takes place only after the whole plant has died and is not covered any more by sand. Saprophagous organisms (Tenebrionidae, etc.) probably facilitate the action of the decomposers.

Ecosystems of monadnocks and canyons

The biotopes of these systems (crevices, debris fans, larger and smaller ravines and runnels, etc.) are manifold. Good rainy years have a prolonged after-effect because water can be stored locally in the ground. Frequency of precipitation and density of vegetation increase with decreasing distance from the escarpment. Numerous larger and smaller consumers can live in this complex of ecosystems, especially where water persists for longer times in rock basins. The klipspringer *Sylvicapra grimmia steinhardti*, many rodents, birds, beasts of prey, etc., can be found there. The food web is most probably very complex but has scarcely been investigated.

Ecosystems of ravines and small riviere

These too are complex but unstable ecosystems, carrying after a rainy year a rich vegetation which becomes increasingly poorer when the available water reserves dwindle. Finally only a few perennial plants, like *Adenolobus*, *Citrullus* and *Parkinsonia*, remain in non-saline riviere, and some halophytes remain in saline riviere.

Oasis ecosystems in the Swakop, Khan and Kuiseb

These ecosystems are complex but relatively stable wherever the riviere carry ground water permanently. This is especially true for the gallery forests formed by *Acacia albida*, *A. giraffae* and other woody plants, which often occur with a herbaceous undergrowth. Phytomass and primary production have not been measured, but production is probably high. The soil is often covered by the nutritious fruits of the *Acacia* trees, and consumers, especially rodents, are numerous. They are eaten by snakes. The watering places are visited by larger wild mammals. In the last century elephants and rhinoceroses were still common, but they have since disappeared from the central Namib. The ecosystems of the river bed proper are very unstable. Each flood destroys the plant cover completely. It re-develops quickly on the humid sand after the flood has passed and the water has infiltrated into the soil.

Ecosystems of the grasslands of the inner Namib

These ecosystems are not very complex. Species of *Stipagrostis* develop after a summer rainfall and are the main primary producers. The main consumers are large herbivorous animals including the ostrich, and certain rodents, but the carnivorous mammals and birds are also important. Primary production certainly fluctuates much from year to year. It was measured by Seely (1978) along a transect 44 km long starting at Gobabeb and running in an ENE direction toward Ganab (see Fig. 7.4). At distances of 2 km, rain gauges were installed and 5 m^2 of vegetation were clipped at ground level on the gravel plain, excluding localities where run-off collects, at randomly selected sites near each rain gauge. Along the whole transect the annual grass *Stipagrostis ciliata* composed 80.6 to 100% of the dry matter, except at 12 km where *S. subacaulis* made up 88.1% of the total phytomass. As none of the areas had supported a grass cover of any extent the previous year, the contribution of phytomass from the previous growing seasons was negligible.

The average annual above-ground phytomass for this specific year amounted to 14.63 g m^{-2} with a variation from zero to 88.68 g m^{-2} (s.d. = 18.99, $n = 100$). This variation is mainly a function of the

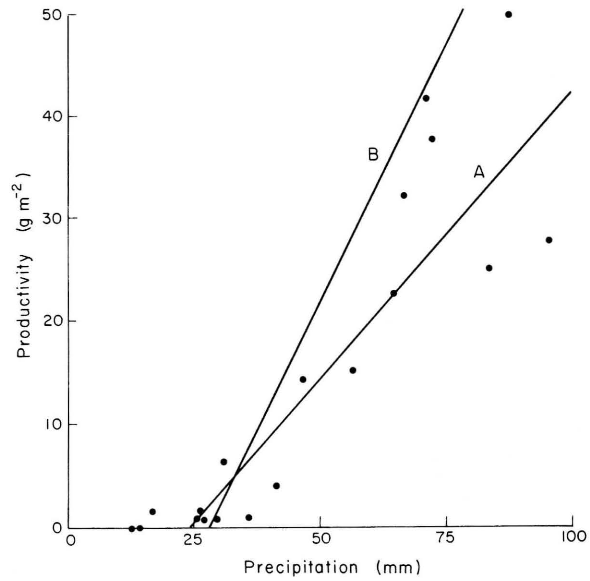


Fig. 7.19. Relationship of grass production to precipitation in the central Namib (A: Seely, 1978) and more mesic Namibia [SW Africa] (B: Walter, 1939).

rainfall. These values are at the lower extreme of reported values for desert vegetation (Noy-Meir, 1973).

The "zero-yield intercept" was 23.1 mm (Fig. 7.19). In this case, as in that described by Walter (1939), there is a linear relationship between precipitation and grass production (Fig. 7.19). The different slopes of the lines may be caused by the fact that Walter's plots contained only perennial grasses, which apparently use water more efficiently because of their developed root system, whereas the annual grasses "waste" water for germination and development of new shoots and roots.

The complete lack of grass species diversity during 1974 was due to the low rainfall, since in 1976, after an unusually heavy rainfall at Gobabeb (98 mm in January to March), many species not normally seen there were growing on the study area.

Ecosystems of dunes without primary producers

Seely and Louw (1980) have provided quantitative data on production energetics of this unusual ecosystem, both for dry years (mean annual precipitation 14 mm) and for the wet year 1976, with

118 mm of rain between January and March. Three biotopes were distinguished:

(1) The dune valleys, representing 55% of the total area, with a gravelly substrate or exposed sandstone, and an ephemeral grass vegetation (*Stipagrostis gonatostachya* and *S. ciliata*) in the wet year only.

(2) The better-consolidated dune slopes, on the windward side or the lower parts of the lee side, constituting 44% of the total, where, even in years of low rainfall, very scattered tussocks of *Stipagrostis sabulicola* or cushions of *Trianthema hereroensis* form a sub-biotope.

(3) The mobile lee-side slopes below the crest of the dunes, where the sand grains blown across it are deposited. This biotope occupies only 1% of the total area.

The starting point for circulation of matter and energy in this ecosystem is the detritus blown in from areas surrounding the dunes, consisting mainly of dead grass material. This is supplemented on the slopes by the production of the *Stipagrostis* tussocks and the *Trianthema* cushions. In wet years, the ephemeral grasses in the dune valleys also play a part.

The total organic dry matter increased in the wet year 1976 by a factor of 2.7 in Biotope 1, by 53.0 in Biotope 2 and by 9.4 in Biotope 3 (through additional import of detritus). Primary production in the persistent *Stipagrostis* tussocks increased by a factor of 2.4, and in the *Trianthema* cushions by 19.0. However, the organic matter occurred only sporadically, limited to particular patches. On the dune slopes, the living tussocks and cushions covered only 1% of the area of Biotope 2, though they constituted 59% of the biomass. The total living and dead dry matter in a single tussock of *S. sabulicola* amounted to 354 g above-ground and 394 g below-ground; the corresponding figures for a *Trianthema* cushion were 408 g and 699 g. Of the detritus on the mobile slopes, 99% occurred at the base.

If the biomass is expressed in terms of the total area of dunes studied, the phytomass in a dry year amounted to only 3 g m^{-2}, the zoomass to 0.01 g m^{-2}. These are the lowest values reported for any ecosystem yet studied. After the wet year, the phytomass increased nine-fold, the zoomass six-fold.

Direct decomposition of the phytomass takes place very slowly, since hydrature conditions are favourable for the poikilohydric decomposers only during fog. Decomposition consequently depends mainly on the saprophagous tenebrionid beetles which eat detritus. They can digest cellulose, but the low nitrogen and phosphorus content of the phytomass is a limiting factor. In consequence, the ratio of phytomass to zoomass is 300:1. On the other hand, dead bodies of animals and their excreta are more easily decomposed.

Whether any similar ecosystems depending on frequent fog occur elsewhere is not known. The only likely area is the dune region of the fog desert in Peru and Chile (see Volume A, Chapter 7). The fauna depends on fog water, as described above (p. 274). For predators, which mostly remain beneath the sand surface during the day, the water content of the prey suffices.

Special ecosystems dependent on the ocean

Habitats of seals on the rocky coast

Seals and sea lions (*Arctocephalus pusillus*) living off fish and other sea food (2–2.5 kg per day) often come ashore, in winter when they moult and in summer for mating and producing their young. The best known rookery is Cape Cross, about 130 km north of Swakopmund, where 120 000 to 150 000 animals congregate. Some 7000 to 7500 young seals 7 to 10 months old are killed annually for their furs. At Wolfsbucht south of Lüderitz Bay an even larger colony exists and there is a small one near Cape Fria in the north (W. Giess, pers. comm.). The rocks of these rookeries are smoothly polished by the seals, and coloured white by their excrement. They are devoid of plants, but decomposers are most probably present.

Guano islands and birds of the coastal belt (communication by H. von Schwind, Swakopmund)

The cold Benguela Current is a rich nutritional source for many birds living off fish and other creatures of the ocean and the coastal belt. Penguins (*Spheniscus demersus*) breed on islands off the southern Namib coast, but their number has lately been diminishing (Berry et al., 1974).

The most important guano birds of the Namibian coast are four species of the numerous cormorants (*Phalacrocorax*). The guano islands (Hollam's Bird Island and Mercury Island in the entrance to Spencer Bay) are rocky, 120 and 370 m high respectively, without vegetation and covered by guano. In the rainless climate the excrement of breeding birds accumulates and is "mined" as fertilizer. The guano layer on Ichaboe Island was 12 m thick before mining was started (Andersson, 1861, in Berry et al., 1974). On an artificial island, a platform in the shallow sea between Swakopmund and Walvis Bay, 1000 t of guano are mined annually, on an area of less than 1500 m^2 (Logan, 1960). Other coastal birds are the pelican *Pelecanus onocrotalus* and the flamingos *Phoenicopterus ruber* and *P. minor*, which appear in large flocks. Their breeding ground is inland in the Etosha Pan. Three species of seagulls (*Larus*) also breed inland, whereas *Morus capensis* breeds on the islands.

The habitats of the African oyster catcher (*Haematopus moquini*), three species of grebes (*Podiceps*) and two species of herons (*Ardea cinerea* and *Egretta garzetta*) are the lagoons and ponds used for salt production. They also breed in the coastal region, which is only partially true for the various species of ducks. Many migrant birds, such as stilts, sandpipers, plovers, terns and swallows, hibernate on the coast of the Namib and sometimes even stay there for one breeding season. These birds play an important role as consumers in the ecosystem of the coastal belt.

Aquatic ecosystems of the lagoons

Sand ridges separate these ecosystems from the open sea, but they are nevertheless dependent upon it. The salt concentration in the lagoons is high but variable because of the high evaporation rate and the frequent afflux of sea water. For the same reason the temperature of the lagoon water fluctuates widely. H. and G. Kunz (1973) investigated these ecosystems, composed of a fairly stable association of *Oscillatoria*, diatoms, Nematoda, *Artemia salina*, *Cletocampus trichotus*, larvae of Diptera and *Bledius* (Staphylinidae), all of which find their optimum growing conditions in a particular zone of the lagoons.

Management options for production and conservation

The largest part of the Central Namib is a protected game reserve administered by the local branch of the South West Africa (Namibia) Bureau of Nature Conservancy and Tourism, located at Windhoek. The natural resources are being exploited. The most important are the diamonds in the closed area of the southern Namib. The uranium mine near Rössing will possibly become of even greater importance. The small copper mines (the Hope mine has been re-opened) are less important. Salt, guano and seal furs are produced on the coast. The economic importance of the coastal towns has been repeatedly stressed.

REFERENCES

Abd El Rahman, A.A. and Batanouny, K.H., 1965. The water output of the desert vegetation in the different microhabitats of Wadi Hoff. *J. Ecol.*, 53: 139–145.

Abel, H., 1954. Beiträge zur Landeskunde des Kaokovelds. *Dtsch. Geogr. Blätter*, 47: 7–120.

Acocks, J.P.H., 1953. Veld types of South Africa. *Mem. Bot. Surv. S. Afr.*, No. 28: 1–192.

Acocks, J.P.H., 1964. Karoo vegetation in relation to the development of deserts. In: D.H.S. Davis (Editor), *Ecological Studies in Southern Africa.* Ser. Monogr. Biol. XIV. W. Junk, The Hague, pp. 100–112.

Adamson, R.S., 1938. Notes on the vegetation of the Kamiesberg. *Bot. Surv. S. Afr., Mem.*, No. 18: 1–25.

Anonymous, 1944. *Weather of the Coasts of Southern Africa, 2.* S. Afr. Air Force, Meteorol. Serv. R. Navy, Cape Town, p. 38.

Batanouny, K.H., 1963. *Water Economy of Desert Plants in Wadi Hoff.* Thesis, Cairo University, Cairo.

Beadle, N.C.W. and Tchan, Y.T., 1955. Nitrogen economy in semi-arid plant communities, I and II. *Proc. Linn. Soc. N. S. W.*, 80: 62–70; 47–104.

Beier, M., 1962. Pseudoscorpionides aus der Namib-Wüste. *Sci. Pap. Namib Desert Res. Stn.*, No. 10: 213–222.

Berry, H.H., Seely, M.K. and Fryer, R.E., 1974. The status of the Jackas Penguin *Spheniscus demersus* on Halifax Island off South Africa. *Madoqua*, 3: 27–29.

Besler, H., 1972. Klimaverhältnisse und klimageomorphologische Zonierung der zentrale Namib (Südwestafrika). *Stuttg. Geogr. Stud., Univ. Stuttgart*, 83: 1–209.

Bornmann, C.H., Elsworthy, J.A., Butler, V. and Botha, C.E.J., 1972. *Welwitschia mirabilis*: Observations on general habit, seed, seedling and leaf characteristics. *Madoqua*, 1.

Bornmann, C.H., Botha, C.E.J. and Nash, L.J., 1973. *Welwitschia mirabilis*: Observations on movement of water and assimilates under föhn and fog conditions. *Madoqua*, 2(63–68): 25–32.

Bornmann, C.H., Moran, M.L., Richardson, C.H., Butler, V., Botha, C.E.J., Nash, L.J. and Button, J., 1974. *Welwitschia mirabilis*: Observations on cuticular efficiency. A comparative study. *Madoqua*, 3: 17–26.

Boss, G., 1941. Niederschlagsmenge und Salzgehalt des Nebelwassers an der Küste Deutsch-Südwestafrikas. *Bioklima*, 1.

Brain, C.K., 1962. Observations on the temperature tolerance of lizards in the Central Namib Desert, South West Africa. *Cimbebasia (Windhoek)*, No. 4: 1–5.

Brain, C.K. and Prozesky, O.P.M., 1962. On the body temperatures of birds collected on the Carp–Transvaal Museum Namib Desert Expedition. *Cimbebasia (Windhoek)*, No. 5: 1–8.

Coaton, W.G.H. and Sheasby, J.L., 1972. Preliminary report on a survey of the termites (Isoptera) of South West Africa. *Cimbebasia (Windhoek)*, No. 2: 129.

Coetzee, C.G., 1969. The distribution of mammals in the Namib desert and adjoining inland escarpment. *Sci. Pap. Namib Desert Res. Stn.*, No. 40: 23–36.

Copenhagen, W.J., 1959. The mass mortality of fish in the Walvis region. *J. S.W. Afr. Sci. Soc.*, 8: 11–12.

D'Hoore, J.L., 1964. *La carte des sols d'Afrique*. Comm. Coop. Tech. Afr., Lagos.

Dittrich, P. and Huber, W., 1974. Carbon dioxide metabolism in members of the Chlamydospermae. In: K. Avron (Editor), *Proc. 3rd Int. Congr. Photosynthesis*. Elsevier, Amsterdam, pp. 1573–1578.

Doidge, E.M., 1946. The South African fungi and lichens. *Bothalia*, 5: 225–376.

Durand, J.H., 1963. Les croûtes calcaires et gypseuses en Algerie: formation et âge. *Bull. Soc. Géol. Fr.*, 7, V: 959–968.

Du Toit, A.L., 1956. *Geology of South Africa*. Oliver and Boyd, Edinburgh, 611 pp.

Franz, H. and Franz, G., 1968. Beitrag zur Kenntnis von Kalkkrusten in Böden der warmen Trockengebiete. *Z. Pflanzenernähr. Bodenkd.*, 121: 34–42.

Gaff, D.F., 1972. Drought resistance in *Welwitschia mirabilis* Hook fil. *Dinteria*, No. 7: 3–7.

Giess, W., 1968. A short report on the vegetation of the Namib coastal area from Swakopmund to Cape Frio. *Dinteria*, No. 1: 13–30.

Giess, W., 1969. *Welwitschia mirabilis* Hook fil. *Dinteria*, No. 3: 3–55.

Giess, W., 1970. Die Verbreitung von *Moringa ovalifolia* Dinter und Berger in Südwestafrika. *Dinteria*, No. 5: 59–64.

Giess, W., 1971. Eine vorläufige Vegetationskarte von Südwestafrika. *Dinteria*, No. 4: 1–14.

Giess, W., 1981. Die in der Zentralen Namib von Südwestafrika/Namibia festgestellten Pflanzenarten und ihre Biotope. *Dinteria*, No. 15: 13–69.

Goudie, A., 1972. Climate, weathering, crust formation, dunes and fluvial features of Central Namib Desert, near Gobabeb, South West Africa. *Madoqua*, 1: 15–32.

Hamilton, W.J., 1969. Thermoregulatory behavior of the vegetarian lizard *Angolosaurus skoogi* on the vegetationless northern Namib desert dunes. *Sci. Pap. Namib Desert Res. Stn.*, No. IV. 95–103.

Hamilton, W.J. and Seely, M.K., 1976. Fog basking by the Namib desert beetle, *Onymacris unguicularis*. *Nature*, 262: 284–285.

Henrici, M., 1926. Growth of veld plants under arid conditions of Betchuanaland. *S. Afr. J. Sci.*, 23: 325 ff.

Henrici, M., 1927. *Physiological Plant Studies in South Africa*. Rep. Director of Vet. Educ. Res., Pretoria, pp. 11–12.

Henrici, M., 1929. Structure of cortex of grass roots in the more arid regions of South Africa. *Dep. Agric. Sci. Bull.*, No. 85.

Henrici, M., 1937. *Transpiration and Water Supply of South African Plants*. Lecture in Windhoek.

Henrici, M., 1940. Transpiration of karoo bushes. *Sci. Bull. S. Afr.*, No. 185.

Henrici, M., 1940b. The transpiration of large karoo bushes. *S. Afr. J. Sci.*, 37: 156–163.

Holm, E., 1969. Contribution to the knowledge of the biology of the Namib Desert golden mole *Eremitalpa granti namibensis* Bauer & Niethammer 1959. *Sci. Pap. Namib Desert Res. Stn.*, No. IV: 37–42.

Jaeger, F., 1965. *Geographische Landschaften Südwestafrikas*. SWA Wiss. Ges., Windhoek, 251 pp.

Jessen, O., 1936. *Reisen und Forschungen in Angola*. Berlin.

Joubert, E., 1971. *Ecology, Behavior and Population of the Hartmann Zebra*, Equus zebra hartmanni *Matischie 1898 in South West Africa*. Div. Nat. Conserv. and Tourism, Windhoek, 176 pp.

Kappen, L., 1975. The lichen symbiosis, a special adaptation to the ecological conditions of extreme environments. In: *XII Int. Bot. Congr., Leningrad.*

Kappen, L., Lange, O.L., Schulze, E.D., Evenari, M. and Buschbom, U., 1975. Primary production of lower plants (lichens) in the desert and its physiological basis. In: J.P. Cooper (Editor), *Photosynthesis and Productivity in Different Environments*. Cambridge University Press, Cambridge, pp. 133–143.

Kers, L.E., 1967. The distribution of *Welwitschia mirabilis* Hook f. *Sven. Bot. Tidskr.*, 61: 97–125.

Knetsch, G., 1960. Über aride Verwitterung unter besonderer Berücksichtigung natürlicher und künstlicher Wände in Ägypten. *Z. Geomorphol., Suppl.*, 1.

Koch, C., 1961. Some aspects of abundant life in the vegetationless sand of the Namib Desert dunes. *Sci. Pap. Namib Desert Res. Stn.*, No. 1. (*J. S. W. Afr. Sci. Soc.*, 15: 8).

Koch, C., 1962a. The Tenebrionidae of Southern Africa, XXXI. Comprehensive notes on the tenebrionid fauna of the Namib Desert. *Sci. Pap. Namib Desert Res. Stn.*, No. X: 61–106.

Koch, C., 1962b. The Tenebrionidae of Southern Africa, XXXII. New psammophilous species from the Namib Desert. *Sci. Rep. Namib Desert Res. Stn.*, No. X: 107–159.

Kühnelt, W., 1965. Nahrungsbeziehungen innerhalb der Tierwelt der Namibwüste (Südwestafrika). *Sitzungber. Österr. Akad. Wiss., Nath. Naturwiss. Kl., Abt. 1*, 174: 185–190.

Kühnelt, W., 1975. Beiträge zur Kenntniss der Nahrungsketten in der Namibwüste (Südwestafrika). *Verh. Ges. Ökol.*, pp. 197–210.

Kunz, H. and Kunz, G., 1973. Ökologische Untersuchungen an Strandgewässern Südwestafrikas. *Namib Meer (Swakopmund)*, 4: 41–64.

Lawrence, R.F., 1932. Spiders of the Namib Desert. *Sci. Pap. Namib Desert Res. Stn.*, No. X: 197–211.

Lawrence, R.F., 1962. Solifuges, Scorpiones and Chilopoda of the Namib Desert. *Sci. Pap. Namib Desert Res. Stn.*, No. X: 213–222.

Lawrence, R.F., 1972. New psammophilous Solifugae, chiefly from the desert region of the Kalahari and South West Africa. *Madoqua*, 1: 97–116.

Lawrence, R.F., 1975. The Chilopoda of South West Africa. *Cimbebasia*, No. 4: 35–45.

Leistner, O.A., 1967. The plant ecology of the southern Kalahari. *Mem. Bot. Surv. S. Afr.*, 38: 1–172.
Leistner, O.A. and Werger, M.J.A., 1973. Southern Kalahari phytosociology. *Vegetatio*, 28: 353–399.
Lempp, F., 1956. Erkundung der Brandberge in Südwestafrika. *Kosmos (Stuttgart)*, 52: 424–436.
Lindner, E., 1971–1973. Zur Kenntnis der Dipteren-Fauna Südwestafrikas, I–III. *J. S.W. Afr. Sci. Soc.*, 26: 85; 27: 73; 28: 73.
Logan, R.F., 1960. The Central Namib Desert, South West Afrika. *Natl. Acad. Sci., Nat. Res. Counc.*, Publ. 758: 162 pp.
Logan, R.F., 1969. Geography of Central Namib Desert. In: W.G. McGinnies and B.J. Goldman (Editors), *Arid Lands in Perspective*. University of Arizona Press, Tucson, Ariz., pp. 128–143.
Louw, G.N. and Hamilton, W.J., 1972. Physiological and behavioural ecology of the ultrapsammophilous Namib Desert tenebrionid *Lepidochora argentogrisea*. *Madoqua*, 1: 87–95.
Louw, G.N. and Holm, E., 1972. Physiological, morphological and behavioural adaptations of the ultrapsammophilous Namib Desert lizard *Aporosaura anchietae* (Bocage). *Madoqua*, 1: 67–85.
Louw, G.N. and Seely, M.K., 1980. Exploitation of fog water by a perennial Namib dune grass, *Stipagrostis sabulicola*. *S. Afr. J. Sci.*, 76: 38–39.
Louw, G.N., Bejonje, P.C. and Coetzee, H.J., 1969. Renal function, respiration, heart rate and thermoregulation in the ostrich (*Struthio camelus*). *Sci. Pap. Namib Desert Res. Stn.*, No. IV: 43–54.
Marloth, R., 1908. Das Kapland. *Wiss. Ergebn. Dtsch. Tiefsee-Exped. Jena*, II, Teil 3.
Martin, H., 1961. Abriss der geologischen Geschichte Südwestafrikas. *J. S.W. Afr. Sci. Soc.*, XV.
Martin, H., 1964. A suggested theory for the origin and a brief description of some gypsum deposits of South West Africa. *Trans. Geol. Soc. S. Afr.*
Martin, H., 1965. *The Precambrian Geology of South West Africa and Namaqualand*. The Precambrian Research Unit, University of Cape Town, Cape Town.
Mattick, F., 1970. Flechtenbestände der Nebelwüste und Wanderflechten der Namib. *Namib Meer (Swakopmund)*, 1: 35–44.
Merxmüller, H., 1972. Prodromus einer Flora von Südwestafrika. 35 Lieferungen. J. Cramer, Lehre.
Muir, J., 1929. The vegetation of the Riversdale area, Cape Province. *Bot. Surv. S. Afr., Mem.*, No. 13: 82 pp.
Noy-Meir, I., 1973. Desert ecosystems: environment and producers. *Annu. Rev. Ecol. Syst.*, 4: 25–51.
Nel, J.A.J., 1969. The prey of owls in the Namib Desert. 1. The spotted eagle owl *Bubo africanis* at Sossus Vlei. *Sci. Pap. Namib Desert Res. Stn.*, No. IV: 55–58.
Newlands, G., 1972. Description of *Hadogenes lawrencei* sp. nov. (Scorpiones) with a check list and key to the South West African species of the genus *Hadogenes*. *Madoqua*, 1: 133–140.
Nieman, W.A., Heyns, C. and Seely, M.K., in press. A note on precipitation at Swakopmund. *Madoqua*.
Nordenstam, B., 1974. The flora of the Brandberg. *Dinteria*, No. 11: 3–67.
Prozesky, O.P.M., 1969. Notes on the daily drinking pattern of certain bird species. *Sci. Pap. Namib Desert Res. Stn.*, No. IV: 69–81.
Range, P., 1930–1938. Flora des Namalandes I–XIII. *Repert. Spec. Nov. Regni Veget.*, pp. 30–44 (Berlin–Dahlem).
Range, P., 1940. Vegetationskarte von Deutsch-Südwestafrika. *Ber. Dtsch. Bot. Ges.*, 58: 226–229.
Ruellan, A., 1967. Individualisation et accumulation du calcaire dans les sols et les dépôts quaternaires du Maroc. *Cah. Pédol., ORSTOM.*
Rust, U., 1970. Beiträge zum Problem der Inselberglandschaften aus dem mittleren Südwestafrika. *Hamburger Geogr. Stud., Inst. Geogr. Univ. Hamburg*, 23.
Sandelowsky, B.H., 1974. Archeological investigations at Mirabib Hill rock shelter. *S. Afr. Archeol. Soc. (Goodwin Ser.)*, 2: 65–72.
Sandelowsky, B.H. and Pendleton, W.C., 1970. Field work at Meob Bay. *Namib Meer (Swakopmund)*, 1: 45–57.
Sauer, E.G.F., 1966. The behavior and ecology of the South African ostrich. *Living bird*, 5: 45–75.
Sauer, E.G.F., 1967. Yawning and other maintenance activities in the South African ostrich. *AUK*, 84: 571–587.
Sauer, E.G.F., 1970. Interspecific behavior of the South African ostrich. *Ostrich, Suppl.*, 8: 91–103.
Sauer, E.G.F., 1971. Die Kurzohrige Elefantenspitzmaus in der Namib. *Namib Meer (Swakopmund)*, 2: 5–43.
Sauer, E.G.F., 1973. Notes on the behavior of Lappetfaced and Cape Vultures in the Namib Desert of South West Africa. *Madoqua*, 2: 43–62.
Scholz, H., 1963. *Studien über die Bodenbildung zwischen Rehoboth und Walvis Bay*. Dissertation, Bonn.
Scholz, H., 1971. Calcretes and their formation. A survey based on observations in South West Africa. *Pedologie (Ghent)*, 21(2): 170–180.
Scholz, H., 1972. The soils of the Central Namib Desert with special consideration of the soils in the vicinity of Gobabeb. *Madoqua*, 1: 33–51.
Scholz, H., 1974. Das Versalzungsproblem der Bewässerungsböden im Unterlauf des Swakops in Südwestafrika. *Z. Kulturtech. Flurbereinig.*, 15: 367–375.
Schulze, E.D., Ziegler, H. and Stichler, W., 1976. Environmental control of Crassulacean acid metabolism in *Welwitschia mirabilis* Hook fil. in its range of natural distribution in the Namib desert. *Oecologia (Berl.)*, 24: 323–334.
Seely, M.K., without year. Dr. Charles Koch Namib Desert Research Foundation. Windhoek, 6 pp.
Seely, M.K., 1973. Factors controlling reproduction of certain Namib Desert tenebrionids. *Madoqua*, 2: 63–65.
Seely, M.K., 1978. Grassland productivity: The desert end of the curve. *S. Afr. J. Sci.*, 74: 295–297.
Seely, M.K., 1979. Irregular fog as a water source for desert dune beetle. *Oecologia (Berl.)*, 42: 213–227.
Seely, M.K. and Hamilton, W.J., 1976. Fog catchment sand trenches constructed by tenebrionid beetles, *Lepidochora*, from the Namib desert. *Science*, 193: 484–486.
Seely, M.K. and Louw, G.N., 1980. First approximation of the effects of rainfall on the ecology and energetics of Namib Desert dune ecosystem. *J. Arid Environ.*, 3: 25–54.
Seely, M.K. and Stuart, P., 1976. Namib climate, 2. The climate of Gobabeb, ten year summary 1962/72. *Transvaal Mus. Bull.*, pp. 7–9.

Seely, M.K., De Vos, M.P. and Louw, G.M., 1977. Fog imbibition, satellite fauna and unusual leaf structure in a Namib desert dune plant *Trianthema hereroensis*. *S. Afr. J. Sci.*, 73: 169–172.

Seydel, R., 1951. Das Schwemmland im Swakop 1913–1943. *J. S. W. Afr. Sci. Soc.*, 8: 13–40.

Shields, L.M. and Drouet, F., 1962. Distribution of terrestrial algae within the Nevada test site. *Am. J. Bot.*, 49: 547–555.

Smith, B.N. and Epstein, S., 1971. Two categories of $^{13}C/^{12}C$ ratios for higher plants. *Plant Physiol.*, 47: 380–384.

Spreitzer, H., 1966. Beobachtungen über Geomorphologie der Zentralen Namib und ihrer Randgebiete. *J. S. W. Afr. Sci. Soc.*, 20.

Stengel, H.W., 1964. Die Riviere der Namib und ihr Zulauf zum Atlantik. Teil I: Kuiseb und Swakop. *Sci. Pap. Namib Desert Res. Stn.*, No. 22: 23–38.

Strassen, W.J. zur, 1971. *The Fur Seal of Southern Africa*. Cape Town, 71 pp.

Sykes, G., 1911. The anatomy and morphology of the leaves and inflorescences of *Welwitschia mirabilis*. *Philos. Trans. R. Soc. Lond., Ser. B*. 201.

Takeda, H., 1913. Some points in the anatomy of the leaf of *Welwitschia mirabilis*. *Ann. Bot.*, 27.

Vedder, H., 1973. *Das alte Südwestafrika*. SWA Wiss. Ges., Windhoek, 686 pp.

Vogel, S., 1955. Niedere Fensterpflanzen in der südafrikanischen Wüste. *Beitr. Biol. Pfl.*, 31: 45–135.

Von Willert, D., Eller, B.M., Brinkmann, E. and Baasch, R., 1982. CO_2-gas exchange and transpiration of *Welwitschia mirabilis* Hook fil. in the Namib Desert. *Oecologia (Berlin)*. 55: 21–29.

Walter, H., 1936. Die ökologischen Verhältnisse in der Namib-Nebelwüste (Südwestafrika) unter Auswertung der Aufzeichnungen des Dr. G. Boss (Swakopmund). *Jahrb. Wiss. Bot.*, 84: 58–222.

Walter, H., 1939. Grasland, Savanne und Busch der arideren Teile Afrikas in ihrer ökologischen Bedingtheit. *Jahrb. Wiss. Bot.*, 87: 750–860.

Walter, H., 1968. *Die Vegetation der Erde, II. Die gemäßigten und arktischen Zonen*. Gustav Fischer, Jena, 1001 pp.

Walter, H., 1971. *Ecology of Tropical and Subtropical Vegetation*. Oliver and Boyd, Edinburgh, 539 pp.

Walter, H., 1973a. *Die Vegetation der Erde. I. Die tropischen und subtropischen Zonen*. Gustav Fischer, Stuttgart, 3rd ed., 743 pp.

Walter, H., 1973b. *Vegetation of the Earth in Relation to Climate and the Ecophysiological Conditions*. Springer, Heidelberg, 237 pp.

Walter, H., 1975. Besonderheiten des Stoffkreislaufs einiger terrestrischer Ökosysteme. *Flora*, 164: 169–183.

Walter, H. and Breckle, S.-W., 1984. *Die Ökologie der Erde–Geo-Biosphäre 2: Spezielle Ökologie der tropischen und subtropischen Zonen*. Gustav Fischer, Stuttgart.

Walter, H. and Kreeb, K., 1970. *Die Hydratation und Hydratur des Protoplasmas der Pflanze*. Protoplasmatologia, II, C/6. Springer-Verlag, Heidelberg, 306 pp.

Walter, H. and Stadelmann, E., 1974. A new approach to the water relation of desert plants. *Desert Biol.*, II: 214–310.

Walter, H. and Walter, E., 1953. Einige allgemeine Ergebnisse unserer Forschungsreise nach Südwestafrika 1952/53: Das Gesetz der relativen Standortskonstanz; das Wesen der Pflanzengesellschaften. *Ber. Dtsch. Bot. Ges.*, 66: 227–235.

Whatley, J.M., 1975. The occurrence of a peripheral reticulum in plastids of the gymnosperm *Welwitschia mirabilis*. *New Phytol.*, 74: 215–220.

Willoughby, E.J. and Cade, T.J., 1967. Drinking habits of birds in the central Namib Desert of South West Africa. *Sci. Pap. Namib Desert Res. Stn.*, No 31: 1–35.

Winter, K., Lüttge, U., Winter, E. and Troughton, J.H., 1978. Seasonal shift from C_3 photosynthesis to crassulacean acid metabolism in *Mesembryanthemum crystallinum* growing in its natural environment. *Oecologia (Berlin)*, 34: 225–237.

Zemke, E., 1939. Anatomische Untersuchungen an Pflanzen der Namibwüste. *Flora, N.F.*, 33: 365–416.

Ziegler, H. and Vieweg, G.H., 1970. Poikilohydre Pteridophyta (Farngewächse). Poikilohydre Spermatophyta (Samenpflanzen). In: H. Walter and K. Kreeb, *Die Hydratation und Hydratur des Protoplasmas der Pflanze*. Protoplasmatologia, II, C/6. Springer-Verlag, Heidelberg, pp. 88–108.