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Climate patterns and their impact on the vegetation in a fog driven desert: The Central Namib Desert in Namibia

by Berit HACHFELD and Norbert JÜRGENS, Cologne

with 10 figures and 2 tables

Abstract. The Central Namib Desert can serve as a model for vegetation-climate related patterns: The landscape exhibits vast plains lacking any strong disturbances. Within the desert, coastal plains are characterised by mild air temperatures, continuously high air humidity by fog and no rain. The opposite is true for the continental eastern part of the desert, where high air temperatures, low air humidity and increasing regularity of summer rainfall prevail. Between both, a zone of most extreme climatic conditions exists with a nearly continuous lack of moisture input by rain or fog, but very high air temperatures and low air humidity. In order to understand the impact of this steep climatic gradient on the vegetatión, an extensive climate monitoring programme has been installed since 1995, comprising automatic weather stations, thermohygrographs and small scale fog measurements along a coast to inland transect of 120 km length. Analysis of both, vegetation and climate, reveal a strong correlation with respect to species richness, total canopy cover, composition of growth forms, and vegetation units. The Minimum Zone in the midst of the desert emphasises the impact climate patterns have on desert vegetation.

Keywords: fog; climatic gradients; species richness; growth forms; classification; Minimum Zone.

Introduction

Climate has a strong impact on the biotic components of a landscape (e.g. FERNANDEZ-PALACIOS 1992; SCHWARZ 1995; LANE et al. 1998). The vegetation in particular, is highly influenced by climatic elements such as precipitation, air temperature and air humidity (e.g. COETZEE & WERGER 1975; SEELY 1978; MILTON 1994; GÜNSTER 1993; SOUTHGATE et al. 1996). For the vegetation in coastal deserts such as the Namib, Atacama or Sonoran Desert, precipitation by fog is often as important as rain (e.g. RUNDEL 1978; ROBINSON 1990; JÜRGENS et al. 1997).

The unique environmental conditions of the Central Namib Desert offer the exceptional opportunity to investigate the impact of major climatic elements on desert vegetation. Due to a homogeneous landscape characterised by predominantly vast plains the climate of the Central Namib comes to its full expression over most of the area. Additionally, the land rises very gradually with only 1 % inclination from coast to inland, a raise in altitude of about 100 m/km, respectively. Within this unique model-like environ-

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ment the different climatic elements show a distinctive variation in their occurrence in space and time.

To date, the paucity of data only allowed broad classifications of several climate and vegetation regions for Namibia (Leser 1976; Giess 1971; van der Merwe 1983). For the Central Namib Desert one to three spatial divisions based on abiotic characters have been differentiated (Besler 1972; Walter 1985). Instead, more attention has been given to special climatic aspects of the Central Namib Desert such as the development and occurrence of fog, rain, different wind systems or boundary layer circulation (e.g. Gülland 1907; Nagel 1959; Tyson & Seely 1980; Lindesay & Tyson 1990; Lengosa et al. 1993; Henschel et al. 1998). Whereas early studies are often restricted to locations of special interest such as to the towns Swakopmund or Walvisbay, recent studies focus on synoptic patterns or are incorporated into geo-scientific and palaeoecologically focused analysis (e.g. Taljaard & Schumann 1940; Heine & Walter 1997).

Also due to the lack of detailed data no comprehensive classification exists for the Central Namib Desert with respect to either a phytosociological or a vegetation ecological approach. The vegetation map of Namibia by Giess (1971) identifies the Central Namib as one coherent vegetation type of a total of four hyperarid vegetation types forming the Namibian part of the Namib Desert. Despite the sparseness of plants the Central Namib cannot at all be described as homogeneous when looking at its vegetation. In contrast, a sequence of several vegetation communities occurs from coast to inland (Hachfeld 1996). There are only few phytosociological studies of the Central Namib Desert which, however, refer to restricted areas only (Moisel & Moll 1981; Robinson 1976; Nel & Oppermann 1985; Schieferstein & Loris 1992). More interest has been evoked by single plant species such as *Welwitschia mirabilis* (e.g. Marsh 1990; Schulze & Schulze 1976).

Only little is known about the steep climatic gradient from the coast to inland and its control of the vegetation. In this study a better understanding of the latter is approached by monitoring a series of the major climatic elements with their spatial and temporal distribution. Data of 5 automatic weather stations placed along a coast to inland transect has been analysed since 1995. Additionally, small scale fog measurements contribute to the understanding of the significance of fog in the desert. This data base has been used to differentiate a number of climatic zones in the Central Namib Desert. Together with a comprehensive investigation of the vegetation, correspondence of climate with vegetation units, vegetation density, species diversity, and growth forms composition is suggested for the dominant plain habitats in the northern part of the Central Namib Desert.

Study area

The hyperarid Namib Desert is situated along the west coast of Southern Africa, where it occupies an elongated tract of only 100–150 km width and 2600 km length from the Olifants River (32° S) in South Africa to the St.

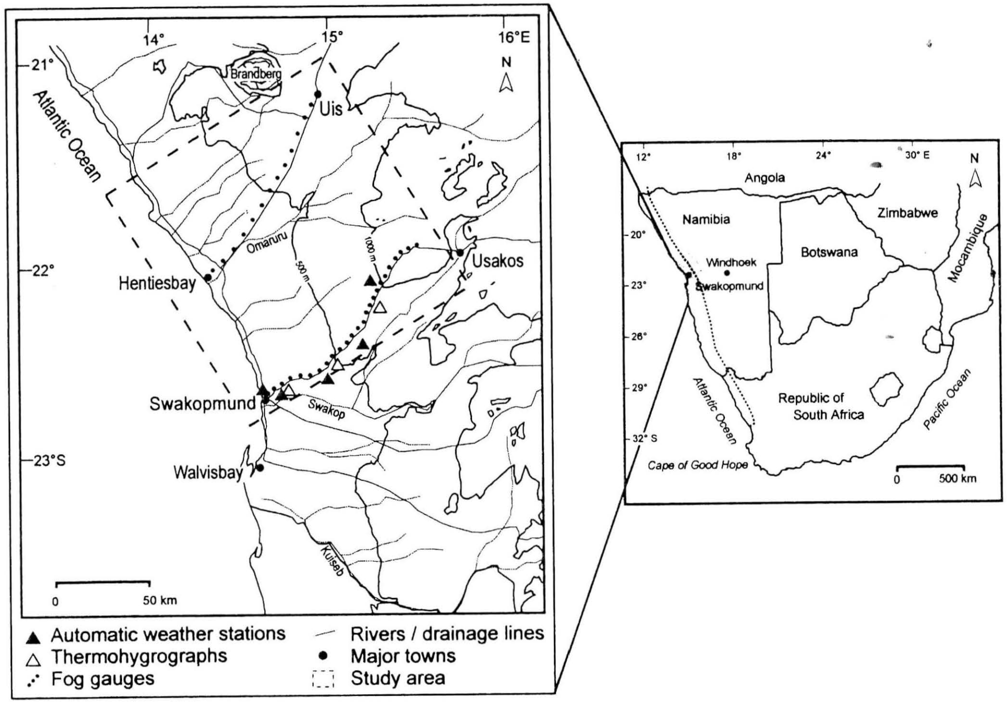

Fig. 1. Right: Map of Southern Africa with Namib (dotted line) and Central Namib Desert (grey box). Left: Map of the study area with position of automatic weather stations, thermohygrographs and fog gauges along 2 coast to inland transects of 120 km length.

Nicolas River (14°20'S) in Angola (Koch 1962). The Central Namib Desert forms its middle part, comprising the area from north of the Great Dune Sea and Kuiseb River to the Huab River (Fig. 1). The paper is concerned with the northern part of the Central Namib Desert, north of the River Swakop, which covers an area of about 18000 km^2 between 21°05'S–22°40'S and 13°50'E–15°15'E.

The climate of the Central Namib Desert is characterised by two major precipitation types: rain and fog. Fog is considered to be the most characteristic climatic feature contrasting the extreme aridity evident in this desert (Olivier 1995). Its formation over the coast is caused by low sea surface temperatures driven by the Benguela Current and the latitudinal position of Namibia within the subtropical high pressure zone. Precipitation by fog in coastal areas can be considerably higher than through rain (Goudie 1972; Henschel et al. 1998). Fog types recognised for the Central Namib include coastal or advective fog forming under a south westerly sea breeze, radiation fog which occurs only occasionally, and high fog. High fog, or Garua fog respectively, is a low stratus and strato cumulus cloud sheet which develops below the inversion layer over the Atlantic Ocean at a height of 100–600 m. From there it penetrates inland and intercepts the land in the Namib interior (LANCASTER et al. 1984; OLIVIER 1995). Whereas the frequency of fog decreases from west to east, frequency and amount of rain increase in the opposite direction. Rain normally falls in form of convective summer storms which can move fairly far into the desert. Thus rainfall is very erratic and highly localised. Mean annual rainfall in the west of the desert is about 23 mm yr^{-1} with a maximum received at the escarpment in the east (GOUDIE 1972). Whereas in the coastal regions climatic conditions are moderate with generally low air temperatures and high air humidity, further inland air temperatures are typically high and air humidity is low.

Topographically, the Central Namib Desert can be ascribed as a weakly undulated and tilted plain, which extends from the Atlantic Ocean in the west to the escarpment in the east. The vast plains are interrupted by a few dry riverbeds (i.e. the Kuiseb, Swakop and Omaruru) and various smaller drainage lines running in east-west direction (SPREITZER 1966; BESLER 1972). Single inselbergs (e.g. Brandberg, Spitzkoppe) as well as small granite outcrops and long-stretched dolerite ridges contribute to the structure of the area. In the northern Central Namib the sudden rise to the escarpment is missing (WALTER 1984). The study area is underlain by rocks of highly metamorphosed nature and of very great age such as rocks of the Damara System, Post-Damara times and Damara metamorphics (GOUDIE 1972). The geological formations comprise predominantly mica schists mixed with marble bands, quartzites and intruded granites (LOGAN 1969). Near the coast gypsum crusts predominate but salt crusts also occur. Further inland crusts consist of limestone. A dense desert pavement covers most of the deserts surface. Soils are generally weakly developed and vary with respect to geology.

The flora of the Central Namib Desert comprises about 415 plant species (GIESS 1981) with a small number of endemics. Lichens contribute considerably to the flora of the coastal region (SCHIEFERSTEIN & LORIS 1992). Phytogeographically, the Central Namib Desert is inhabited by species from both, the Succulent Karoo Region (Greater Cape Flora) along a narrow coastal strip and the Nama Karoo Region further inland (Palaeotropis) (JÜRGENS 1991).

Methods

Climate

Along a coast to inland transect a monitoring program was started in 1995 comprising 5 automatic weather stations at the following distances to the coast: 0 km, 12 km, 35 km, 56 km, 92 km (Fig. 1). Data of the station at km 56 was contributed by the Rössing Uranium Mine. Each station collects

data in a 30-minute turn on air temperature, air humidity, wind direction, wind speed, and total precipitation. Rain gauges are supplied with additional fog collectors similar to others used in this study. Precipitation measured thus includes fog, fog-drizzle and rain with an accuracy of 0.1 mm. Due to sporadical technical problems time series covered by the automatic stations are not continuous (Table 1). The year 1996 was omitted.

Additional thermohygrographs contributed monthly data on air temperature and air humidity at 3 coastal distances along the same transect since 1994 (Fig. 1): 12 km (22°35'S, 14°35'E), 40 km (22°32'S, 14°52'E) and 80 km (22°16'S, 14°07'E). Also along this transect a parallel series of 24 pairs of simple fog and rain gauges contributed weekly information on the small scale distribution of precipitation (Fig. 1). The series starts in Swakopmund at 0 km (22°40'S, 14°33'E) and stretches to 120 km coastal distance (22°00'S, 15°20'E) with a distance of 5 km between each. Whereas in 1995, 1997 and 1998 measurements were only done from February to May, in 1999 a complete year was documented. In the dry season (June to December) measurements ended at 70 km coastal distance. The construction of the gauges principally follow SCHIEFERSTEIN (1989): In an insulated 1-l bottle a plastic funnel (15 cm diameter) is inserted. For the fog gauges an additional bunch of 45 stainless wires each with a length of 35 cm was placed in the funnels. Few drops of oil in the bottles prevent collected water from evaporating during the week. The amount of fog collected was calculated by subtraction of the amount of water in the fog gauge by the amount of water collected in the rain gauge. For a better comparison of the data with that of the climatic stations, the collected amounts in ml were transferred into mm with 25.45 ml equalling 1 mm of either fog or rain.

Vegetation analysis

In the study area 104 relevés on plain habitat sites were sampled from 1995 to 1999. There, species inventory, projected canopy cover by each species and growth forms composition were estimated in 0.1 ha (20*50 m) relevés.

Table 1. GPS-positions of automatic weather stations and available months with data for 1995, 1997–1999.

Climatic station/ months with data	km 0	km 12	km 35	km 56	km 92
GPS	S 22°35' E 14°31'	S 22°38' E 14°38'	S 22°34' E 14°47'	S 22°24' E 15°05'	S 22°10' E 14°10'
1995	3–9	3–11	3–7	1–12	3–4
1997	1–12	1–12	1–12	1–12	1–12
1997	1–12	1–12	1–12	1–12	1–12
1998	1–12	1–12	1–12	1–12	1–12
1999	1–8	3–8	1–8	1–8	1–8

Coverage was estimated in percentage starting with a percentage as low as 0.01 %. Growth form composition comprised the major growth form types, i.e. phanerophytes, chamaephytes, hemicryptophytes, and annuals sensu MÜLLER-DOMBOIS & ELLENBERG (1974). Succulent and non-succulent species as well as stem and leaf succulence were also differentiated. The phytosociological analysis of the data was carried out with the programme TWINSPAN from the Cornell Ecology Programs (HILL 1979). Taxon plant names follow CRAVEN (1999).

Results

Climate

As shown for the data of the automatic weather stations, total precipitation varied strongly within the study area from 1995–1999 (Fig. 2). At the coastal station (km 0) the monthly amount of precipitation was predominantly 2–4 mm with a maximum of 25 mm in September 1998. The amount of precipitation per 30-minute reading was very low (0.1–0.4 mm) and was typically measured throughout the night or early morning hours. Because of that and as the main season for precipitation was winter, i.e. from May to August, precipitation at the coast is considered to be either fog or fog-drizzle. Additionally, precipitation occurred with a very high regularity every month. In contrast, at the stations at km 12 and km 35, for several months no precipitation was measured. Monthly amounts of precipitation were less than at the coast with predominantly 0.2–2 mm at the station at km 12 and 1–5 mm at km 35. Whereas at the more western station (km 12) the main season for precipitation appears to be similar to the coast, at the station at km 35 a clear temporal assignment is not possible. A tendency towards precipitation during summer is suggested though. Further to the east, at the stations of 56 km and 92 km coastal distance, monthly precipitation becomes more sporadic. Single precipitation events dominated which typically lasted from half an hour to a few hours only. At km 56 the monthly amount of precipitation was between 0.5–25 mm. Higher precipitation occurred at 92 km coastal distance varying from 0.1–80 mm per month. Precipitation for both stations is assigned to rain as it was clearly restricted to summer, i.e. December to May.

Comparison of the annual yield of precipitation over the past 5 years shows the importance of fog in the Central Namib Desert: At the coast, total annual precipitation – being mostly fog or fog-drizzle – was as high as 15–64 mm yr^{-1}. Further inland (fog-) precipitation decreases to 7–20 mm yr^{-1} at 12 km and 4–53 mm yr^{-1} at 35 km coastal distance. Towards the east of the study area total precipitation increases again: At km 56, where summer rain prevails, annual amounts between 7–46 mm yr^{-1} correspond with those of the more western stations (km 12, km 35) where fog dominates. But at 92 km coastal distance annual rain amount varied strongly between 3–160 mm yr^{-1}, thus being temporarily even less than at the fog-dominated coast.

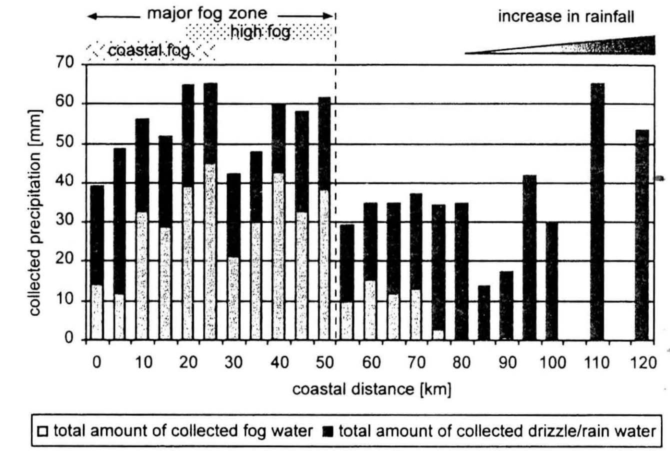

Fig. 3. Total amount of weekly collected fog/fog-drizzle/rain water measured every 5 km along a coast to inland transect in 1999. Shown is the major fog zone with spatial distribution of coastal and high/Garua fog and the extent of increase in rainfall amount towards the eastern border of the desert.

Total amounts of fog, fog-drizzle or rain (Fig. 3) collected weekly in small scale measurements in 1999 show that beyond 50 km coastal distance total precipitation decreases drastically. This distance to the coast marks the end of the major fog zone in the study area. Only rarely fog penetrates as far inland as 70–75 km. The water amounts collected in the rain gauges near the coast are assigned to fog-drizzle as no rainfall was reported by the automatic weather stations for the measuring period. Fog-drizzle, which is characterised here as wet fog, occurs throughout the western part of the desert, up to km 75 with a maximum close to the Atlantic Ocean at km 0 (25 mm) and km 5 (35 mm). Further inland fog-drizzle is not evident anymore and precipitation comprises rain only.

The fog amounts collected in the fog gauges show that a transition zone exists between 10–30 km coastal distance in which coastal fog as well as high/Garua fog occur. No clear assignment to either fog type was possible in this area, but personal observation and the sudden decrease in collected fog water at km 25 suggest that the border between both typically lies at 25 km coastal distance. As shown for two exemplary weeks in 1999, the major fog types, i.e. coastal fog and high/Garua fog, appear mostly in clear spatial patterns (Fig. 4 and 5). They are often accompanied by fog-drizzle of which no clear distinction in either fog type can be made.

Even though annual rain and fog amounts in 1999 (Fig. 3) seem to be quite high for a desert, weekly moisture input by fog – not only for 1999 but also for the other years fog was collected in – is as low as 0.5–2 mm with a maximum of 3–4 mm (Fig. 4).

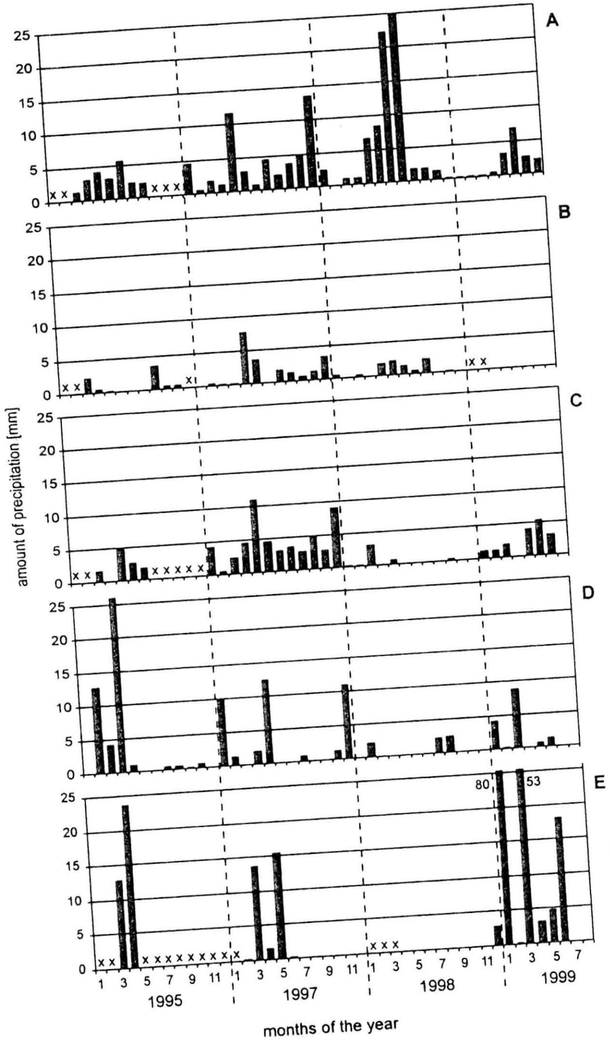

Fig. 2. Total monthly precipitation measured at 5 automatic weather stations along a coast to inland transect for the period of 1995 and 1997–1999 in the following coastal distances: A: 0 km; B: 12 km; C: 35 km; D: 56 km; E: 92 km. Crosses symbolise months without data.

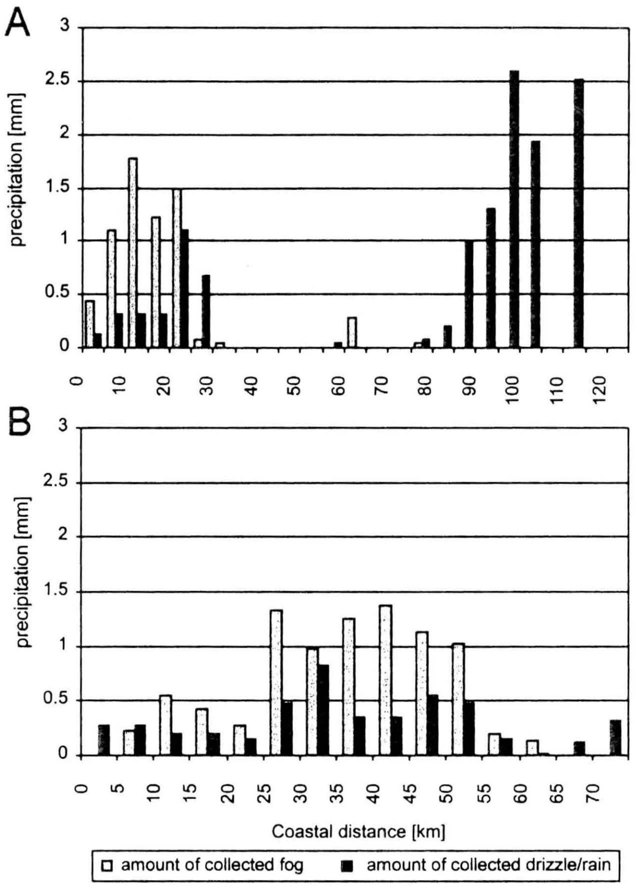

Fig. 4. Two exemplary weekly measurements of fog/fog-drizzle/rain collected with fog and rain gauges along a transect show the 2 dominant fog types in the Central Namib Desert and inland rainfall. A: week of 22.4.–27.4.1999 (coastal fog); B: week of 19.5.–26.5.1999 (high/Garua fog).

Besides precipitation air temperature and air humidity have an impact on the vegetation. In Fig. 6, the daily courses are shown for an exemplary summer day in March 1995. Although air temperature rises and humidity decreases at all weather stations with sunrise, at the coast the fog layer prevents both from changing as fast as inland. At midday air temperatures at the coast are only little higher than night temperatures at the station at 92 km coastal distance. There is no continuous increase in the air temperature with an increase in coastal distance but a leap in the midst of the

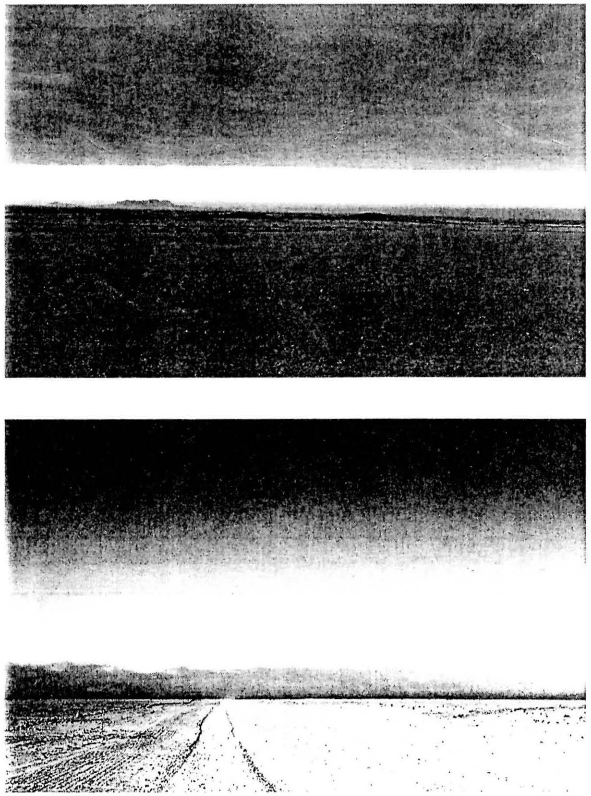

Fig. 5. Top: Photo of a coastal fog front. Bottom: Photo of high/Garua fog in the Central Namib Desert.

desert at km 35. Temperatures here are almost as high as at 92 km coastal distance. In contrast, the air humidity exhibits a significantly high difference between the stations of km 0 and km 12 throughout the day. Highest amplitude in both, air temperature and air humidity, occurs at the station at 35 km coastal distance. This suggests that for the vegetation extreme conditions exist in this coastal distance.

The frequency in which high air temperature and low air humidity occurs is a valuable index for climatic impact on the vegetation. In Fig. 7, mean frequencies in the occurrence of air temperatures over 30 °C, 35 °C and 40 °C as well as air humidity below 20 %, 40 % and above 70 % are shown for the data of 3 thermohygrographs at 12 km, 40 km and 80 km coastal distance over the past 6 years (1994–1999). With a frequency of 73 % yr^{-1} air temperatures above 30 °C occur predominantly in the middle and eastern part of the desert (km 40, km 80). At 40 km coastal distance

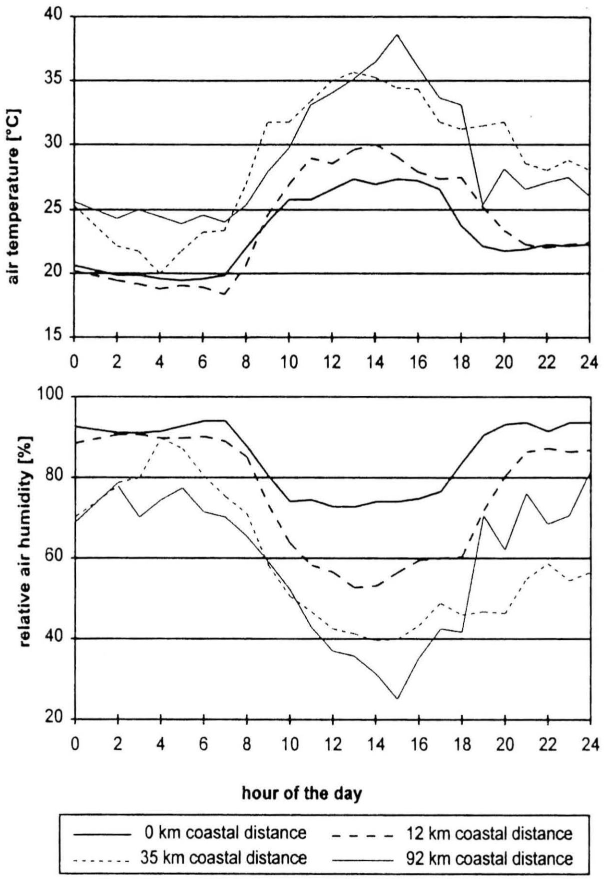

Fig. 6. Daily course of air temperature and air humidity at 4 automatic weather stations in different coastal distances (0 km, 12 km, 35 km, 92 km) for the 14.3.1995.

maximum daily air temperatures above 35 °C were measured with the highest frequency in the study area at 36 % yr^{-1}. In contrast, air temperatures near the coast (km 12) are only high when hot and dry easterly winds (bergwind) reach the coast. Such winds temporarily develop inland in high altitude. These winds blow down the Namib plains towards the coast and are typically paired with high wind speeds and an adiabatic increase in air temperature. As these winds usually do not reach further westwards than 30–40 km coastal distance, air temperatures above 35 °C were measured only at 17 % yr^{-1} near the coast (km 12).

The relative air humidity, on the other hand, is highest near the coast with a humidity above 70 % on 75 % yr^{-1}. In greater coastal distances the

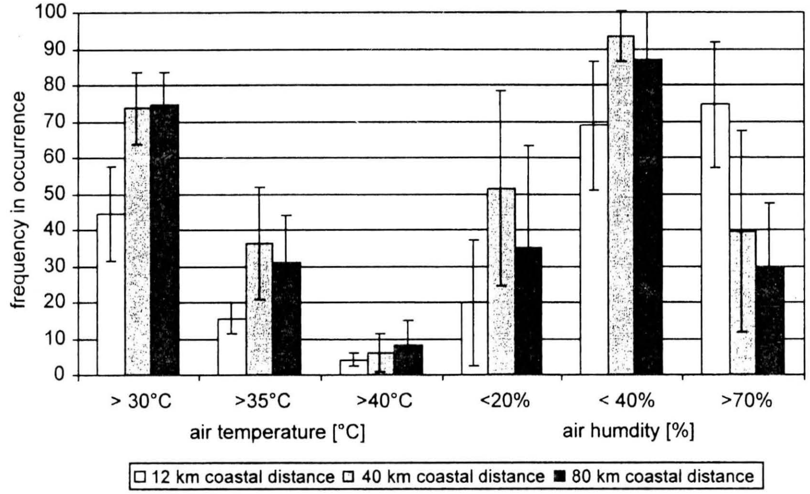

Fig. 7. Frequency of maximum air temperature, maximum and minimum air humidity along a coast to inland transect measured at 3 thermohygrographs placed in different coastal distances (20 km, 40 km, 80 km). Time period covered is 1994–1999.

impact of the Atlantic Ocean and the Benguela Current is less strong and thus humidity there is generally lower. As fog (high/Garua fog) penetrates from the coast inland, at 40 km coastal distance an air humidity above 70 % occurs with a frequency of 39.7 %. In contrast, at km 80, where high/Garua fog does not occur anymore, only at 29.3 % yr^{-1} maximum air humidity is above 70 %. Due to the hot easterly winds air humidity can be very low at all coastal distances. The most extreme conditions for the vegetation were found in the midst of the desert (km 40) where air humidity was below 40 % at 93.5 % yr^{-1}. There, half of the year (51.5 %) minimum daily air humidity is even less than 20 %. In some years, e.g. 1995, such low values can exist for most days (91 %). Further inland air humidity is also predominantly low but not that extreme. On average at 87 % yr^{-1} air humidity is below 40 %, but only during one third of the year it stays below 20 %.

Summarising, the climatic conditions in the northern Central Namib Desert can be described as follows: At the coast, precipitation predominantly occurs in winter as fog or fog-drizzle with a very high regularity. The main fog zone extends to 50 km coastal distance with a spatial differentiation in coastal fog (0–30 km) and high/Garua fog (25–50 km). Both fog types contribute about the same amount of water and annual amounts exceed those of rain in the study area. For the air temperature and air humidity a different spatial pattern was found: Whereas at the coast air temperature is typically mild and air humidity is high, already at 35 km coastal distance climatic conditions are more harsh. Here exists the highest daily frequency of maximum air temperatures and minimum air humidity. This zone stretches beyond the fog zone up to 80–90 km inland. From 50–80 km coastal distance neither fog nor rain contribute significant amounts of water to the vegetation. Only very sporadic single rain events reach into this zone. The high frequencies of high air temperatures and low humidity intensify the harsh environmental conditions for the vegetation. Towards the eastern border of the desert precipitation by rain increases but is still highly sporadic in time and space. Air temperature is typically high and air humidity is low.

Vegetation

Species number as well as total canopy cover of the plains (Fig. 8) show a distinct pattern with respect to coastal distance. Species number (lichens occurring in high diversity near the coast are not included) remains low with values below 7 species/0.1 ha up to a coastal distance of 75 km. Only occasionally after rare and isolated rainfall events more species, namely annual grass species, can be found. Further inland species number varies stronger depending on microhabitat conditions such as rainfall amount in the year of documentation as well as soil and bedrock conditions of the plains. Species richness can be as high as 35 species/0.1 ha. Another differentiation line can be drawn at 100 km coastal distance. East of this line species number stays above 10 species/0.1 ha with typically higher values and a maximum of 54 species after very good rainfall in 1995. This part of the study area marks the transitions zone from desert to savanna vegetation.

In contrast to species number, total canopy cover (including lichens) shows an extreme curvy shape with a distinct minimum in the midst of the Namib Desert. Near the Atlantic Ocean canopy cover can be as high as 10–20 % due to the prevalence of leaf-succulent chamaephytes such as *Zygophyllum clavatum* which occur in large cushions along the coast. From 5–25 km coastal distance lichens contribute to a great extent to the partly high canopy cover. Extremely high cover values (25 %, 39 %) occur in the vast lichen field near Wlotzkasbaken (Fig. 9), which reaches from the coast to about 35 km inland (see SCHIEFERSTEIN 1989).

From 25–75 km coastal distance canopy cover is at its minimum with values predominantly below 1 %. Spatially isolated small chamaephytes (which are often leaf-succulent) typically characterise the vegetation in this part of the desert. Only after rare and spatially very located rainfall an annual grass cover develops and total canopy cover can reach higher values (5–20 %). A similar but not that extreme tendency can be found in the more eastern part of the study area up to a coastal distance of 100 km. In contrast to the latter single rain clouds reach more often this far (75–100 km) into the desert. In years with low rainfall the vegetation has a low canopy cover and comprises sparsely distributed perennial species only. These are typically stem-succulent, small phanerophytic species or large chamaephytic species such as *Calicorema capitata* or *Euphorbia damarana*. In good rainy seasons, however, canopy cover can be higher due to the occurrence of additional ephemeral species. The highest canopy cover val-

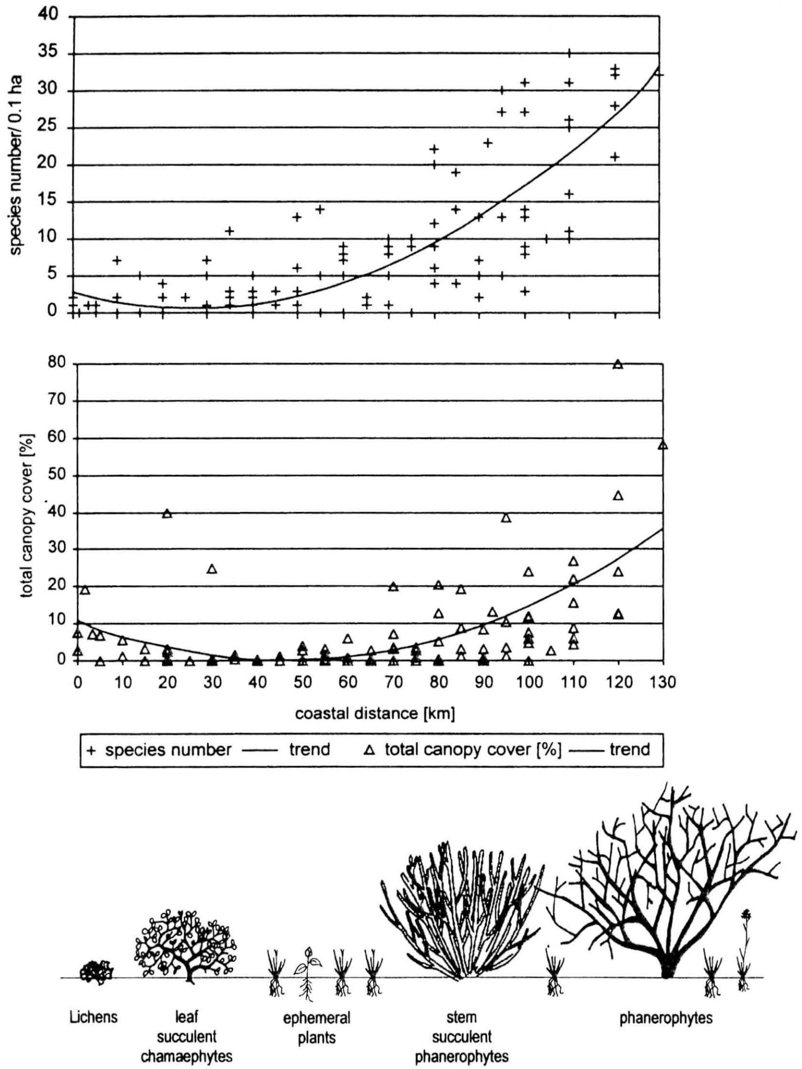

Fig. 8. Species number, total canopy cover and dominant growth forms in relation to coastal distance.

ues (up to 80 %) were found in the transition zone from desert to savanna east of 100 km coastal distance. Larger phanerophytic species predominate the vegetation, which are in good rainy years accompanied by a annual grass and herb cover.

The classification of the vegetation (Table 2) differentiates 6 major vegetation zones with 14 vegetation units for the northern Central Namib Desert. The zones and units alternate from west to east as shown in the vegetation map of the study area (Fig. 9). The Lichen Zone in the west stretches from the coast to a maximum of 50 km inland. This zone comprises 4 vegetation units, each characterised by lichen species. Units A and B represent the lichen field of Wlotzkasbaken of which unit A (*Teloschistes capensis* Unit), having a high canopy cover (14 %), is located near the coast. Here, predominantly fruticose lichens such as *Teloschistes capensis* and *Xanthoparmelia walteri* dominate. Unit B (*Lecidua* spec.-*Combea mullusca* Unit) forms the extended part of the lichen field with a lower canopy cover (2.2 %) and less dominance of fruticose lichens. From there, up to a coastal distance of 50 km vegetation is mainly composed of crustose lichens with a low canopy cover (<1 %), such as *Caloplaca elegantissima*, which grow directly on substrate or boulders (*Caloplaca elegantissima-Xanthoparmelia walteri* Unit). In the *Caloplaca elegantissima* Unit situated in the alluvial plains of the Omaruru River, very large cushions of *Salsola nollothensis* dominate next to crustose lichens. Occasionally *Arthraerua leubnitziae* occurs between the lichens which is the characteristic species of the *Arthraerua leubnitziae* Zone (Fig. 10). This zone also stretches from the coast to 50 km inland and thus forms a spatial pattern with the Lichen Zone. The *Arthraerua leubnitziae-Salsola nollothensis* Unit of this zone comprises large cushions of leaf succulent species along the Atlantic coast line. The other unit (*Arthraerua leubnitziae-Zygophyllum stapfii* Unit) represents the typical composition of vegetation (irrespective of the unique lichen field) in this coastal distance. It is also characterised by a low canopy cover (<1 %).

Beyond 50 km coastal distance a distinct border exists. Here, the *Zygophyllum stapfii* Zone begins and no more *Arthraerua* plants are found. The only vegetation unit of this zone (*Zygophyllum stapfii-Commiphora saxicola* Unit) comprises low species numbers and a canopy cover of 1 % only. This zone and part of the latter belong to the zone with a minimum in vegetation cover and species number in the study area (Minimum Zone, Fig. 8). The adjacent Annual Grassland Zone (Fig. 10) with 2 vegetation units (*Stipagrostis uniplumis-Stip. obtusa* Unit; *Zygophyllum cylindrifolium-Stip. hochstetteriana* Unit) also contribute to the Minimum Zone, representing the further inland-lying part where influence by fog does not occur anymore. Species composition comprises mainly ephemeral *Stipagrostis* species which occur after sporadic rainfall only. In the *Euphorbia damarana* Zone (Fig. 10) 3 vegetation units were differentiated. Depending on the accompanying species one unit (*Euphorbia damarana-Zygophyllum stapfii* Unit) still belongs to the Minimum Zone with a minimum in vegetation cover (2 %) and species richness (3 species/0.1 ha). The other units mark the transition to the less dry parts of the desert (*Euphorbia damarana-Eragrostis nindensis* Unit; *Euphorbia damarana-Calicorema capitata* Unit). In the latter two canopy cover can be high (22–40 %) due to especially ephemeral plants.

Table 2. Vegetation table (shortened) based on a TWINSPAN classification with 6 vegetation zones comprising 15 vegetation units. Shown is the coastal distance, height above sea level, mean species number, mean canopy cover of each unit, and the growth forms of each species in the study area. Vegetation units are: A: *Teloschistes capensis* Unit; B: *Lecidua* spec.-*Combea mollusca* Unit; C: *Caloplaca elegantissima-Xanthoparmelia walteri* Unit; D: *Salsola nollothensis-Caloplaca elegantissima* Unit; E: *Arthraerua leubnitziae-Salsola nollothensis* Unit; F: *Arthraerua leubnitziae-Zygophyllum stapfii* Unit; G: *Zygophyllum stapfii-Commiphora saxicola* Unit; H: *Euphorbia damarana-Zygophyllum stapfii* Unit; I: *Euphorbia damarana-Eragrostis nindensis* Unit; J: *Euphorbia damarana-Calicorema capitata* Unit; K: *Stipagrostis uniplumis-Stip. obtusa* Unit; L: *Zygophyllum cylindrifolium-Stip. hochstetteriana* Unit; M: *Calicorema capitata-Monsonia umbellata* Unit; N: *Boscia foetida-Tribulus zeyheri* Unit. Abbreviations for canopy cover are: 1 = 0–0.1 %; 2 = 0.1–5 %; 3 = 0.5–1 %; 4 = 1–2 %; 5 = 2–5 %; 6 = 5–10 %; 7 = >10 %.

Life form	Vegetation zone	*Calicorema capitata* Zone		annual Grass. Zone		*Euphorbia damarana* Zone			Zygo. stapfii Zone	*Arthraerua leubnitziae* Zone		Lichen Zone			
	Species / Vegetation unit	**N**	**M**	**L**	**K**	**J**	**I**	**H**	**G**	**F**	**E**	**D**	**C**	**B**	**A**
P	Acacia erubescens	6 - -	- - - -	- -	- -	- - -	- - -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
H	Geigeria ornativa	4 - -	- - - -	- -	- -	- - -	- - -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
T	Enneapogon cenchroides	1 - -	- - - -	- -	- -	- - 1	- - -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
Ch	Barleria lancifolia	2 - -	- 1 - -	- -	- -	- - 1	- - -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
T	Acrotome fleckii	1 - 1	- - - -	- -	- -	- - -	- - -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
T	Talinum caffrum	2 - 1	- - - -	- -	- -	1 - -	- - -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
T	Monsonia senegalensis	3 1 -	- - - -	- -	- -	- - -	- - -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
T	Aristida adscensiones	1 1 -	- - - -	- -	- -	- - -	- - -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
T	Setaria verticillata	1 1 -	- - - -	- -	- -	- 2 -	- - -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
T	Limeum argute-carinatum	1 4 -	- - - -	- -	- -	1 - 1	- - -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
T	Amaranthus schlichtianus	1 1 -	4 - - -	- -	- -	- - -	- - -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
Ch	Aptosimum lineare	1 - -	1 1 - -	- -	- -	- - -	- - -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
P St succ	Commiphora dinteri	3 - -	1 2 - -	- -	- -	1 - -	- - -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
T	Cleome semitetrandra	1 - -	1 1 - 1	- -	- -	- - -	1 - 1	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
G	Dipcadi crispum	- - -	1 1 1 -	- -	- -	1 - -	- - -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
H	Oropetium capense	- - -	1 1 1 -	- -	- -	- - -	1 - -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
T	Heliotropium tubulosum	1 - -	1 - 1 1	- -	- 1	- - -	1 1 -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
T	Gisekia afrikana var. africana	1 1 -	- 1 4 -	- -	- -	- - -	- - -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
T	Anticharis senegalensis	1 - 1	1 1 - -	- -	- -	- - -	- - -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
P	Maerua schinzii	1 4 1	- - - -	- -	- -	- - -	- - -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
Ch	Tribulus zeyheri	2 1 1	1 - - -	- -	- -	- - -	- - -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
P	Boscia foetida	5 2 4	1 - - -	- -	- -	- - -	1 4 -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
T	Euphorbia glanduligera	1 1 1	1 - - 1	- -	- -	1 1 1	- - -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
T	Hermannia modesta	1 4 1	1 1 1 -	- -	- -	- - -	- 1 -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
T	Blepharis grossa	2 1 -	1 2 1 1	- -	- -	1 - 1	1 1 -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
H	Eragrostis nindensis	2 - 1	4 2 5 2	- -	- -	1 - 1	4 1 1	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
T	Enneapogon desvauxii	1 - 1	1 1 1 1	1 -	3 -	1 - 1	1 - 4	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
Ch	Monechma genistifolium	4 - 2	3 3 1 1	1 -	- -	1 - 1	1 1 -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
T	Monsonia umbellata	6 1 1	1 5 2 5	- -	- -	- 2 1	- 1 -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
P St succ	Calicorema capitata	1 5 -	2 3 4 2	3 -	- -	4 3 3	- - -	- 1	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
T/H	Stipagrostis ciliata	- - -	5 6 - -	1 5	- -	- - -	1 - -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - 1 -	- - -	- -
T/H	Stipagrostis obtusa	- - -	1 1 - -	1 5	- -	- - -	1 - 5	1 -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
H	Stipagrostis uniplumis v. uniplumis	- - -	- - - -	7 7	- -	- - -	- - -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
T	Stipagrostis subacaulis	- - -	- - - -	- 5	- -	- - -	- - -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
H	Stipagrostis hochstett. v. hochst.	5 - -	- - - -	- 5	- -	1 - 1	- - -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
H	Stipagrostis hochstett. v. secalina	5 - -	- - - 1	- -	5 -	- - -	- - -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
T	Indigastrum argyroides	- - -	1 - - 1	- -	- 1	- - -	1 - -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
T Bl succ	Zygophyllum cylindrifolium	- - -	1 - - -	- -	1 1	- - 1	- 1 1	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
P St succ	Commiphora namaensis	- - -	- - - -	- -	- -	5 - 4	- - -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
H	Indigofera heterotricha	1 - -	- - - -	- -	- -	1 - 1	- 1 -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
Ch	Adenolobus pechuelii	- - 1	- - - -	- -	- -	- - 1	- - -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
H	Stipagrostis giessii	- 7 -	- - - -	- -	- -	- - 6	- - -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
H	Sesamum capense	- 1 -	- - - -	- -	- -	- 1 -	- - -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
Ch	Hirpicium gazanioides	- - -	- - - -	- -	- -	- 1 1	- - -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
H	Geigeria alata	- - -	- - 1 -	- -	- -	1 1 1	- - -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
Ch	Petalidium variabile	- - 2	- - - -	- -	- -	2 1 1	- - -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
P	Acacia reficiens	- - 6	- - - -	- -	- -	3 5 5	- - -	- -	- - - -	- - - - - - 2 - - - -	- -	- -	- - - - -	- - -	- -
H	Stipagrostis schaeferi	- 1 -	1 - - -	- -	- -	7 7 -	2 - 1	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
H/T	Cleome foliosa var. foliosa	- 1 1	- 1 1 -	- -	- -	- 1 1	1 - -	1 -	- - - -	1 - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
T	Euphorbia phyllocladia	- - -	- - 1 -	1 -	- -	1 1 1	1 1 -	- -	- - - -	- - - - - 1 - - 1 - -	- -	- -	- - - - -	- - -	- -
Ch Bl succ	Salsola aphylla	- - -	1 1 1 -	- -	- -	- - -	- 1 1	- -	- 2 - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
H	Kissenia capensis	- - -	- - 1 -	- -	- -	- - -	- 1 -	1 1	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
P St succ	Euphorbia damarana	- 3 -	- - - -	- -	- -	- 4 5	4 5 4	4 4	1 - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
Ch	Monechma cleomoides	- - 1	- - - -	- -	- -	- 1 -	1 - -	- -	- 2 - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
Ch St succ	Commiphora saxicola	- - -	- - - -	- -	- -	- 3 3	- - -	- -	2 2 1 -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
Ch Bl succ	Aloe asperifolia	- - -	- - - -	- -	- -	- - -	- - -	- 3	2 2 - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	- -
Ch Bl succ	Zygophyllum stapfii	- - -	- - - -	- -	- -	- - -	- - -	2 1	2 2 1 1	4 2 2 1 1 1 1 1 1 - -	- -	- -	- - - - -	- - -	- -
Ch St succ	Arthraerua leubnitziae	- - -	- - - -	- -	- -	- - -	- - -	- -	- - - -	5 4 2 4 2 2 1 1 1 1 2	5 6	3 -	- - 1 2 1	- - -	1 -
Ch Bl succ	Salsola nollothensis	- - -	- - - -	- -	- -	- - -	- - -	- -	- - - -	- - - - - - - - - - -	- 5	4 5	- - - - -	- - -	- -
Lich	Caloplaca elegantissima	- - -	- - - -	- -	- -	- - -	- - -	- -	- - - -	- - - - - - - - - - -	- -	5 4	- 1 1 1 2	3 1 2	2 1
Lich	Caloplaca spec.	- - -	- - - -	- -	- -	- - -	- - -	- -	- - - -	- - - - - - - - - - -	- -	5 1	1 - 1 1 2	2 2 2	4 2
Lich	Xanthoparmelia walteri	- - -	- - - -	- -	- -	- - -	- - -	- -	- - - -	- - - - - - - - - - -	- -	1 1	1 1 1 1 1	2 2 1	5 7
Lich	Lecidea spec. 4459	- - -	- - - -	- -	- -	- - -	- - -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - 1	2 5 4	- -
Lich	Combea mollusca	- - -	- - - -	- -	- -	- - -	- - -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	2 3 4	4 4
Lich	Ramalina maculata	- - -	- - - -	- -	- -	- - -	- - -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - -	- - -	1 4
Lich	Teloschistis capensis	- - -	- - - -	- -	- -	- - -	- - -	- -	- - - -	- - - - - - - - - - -	- -	- -	- - - - 1	- - -	4 6
	Coastal distance [km]	120-130	85-110	90	70-80	100-120	85-110	65-70	55-70	15-50	0	10-20	5-50	10-20	1,5-3,3
	Height above sea level [m]	750-1150	800-1050	800	600-750	650-800	750-800	650-700	50-650	50-500	0	0	50-400	100-200	0-20
	Mean species number	3	4	5	8	4	3	2	4	9	2	5	4	6	8
	Mean canopy cover [%]	58	13	3	20	45	22	2	1	4	8	6	< 1	2	14

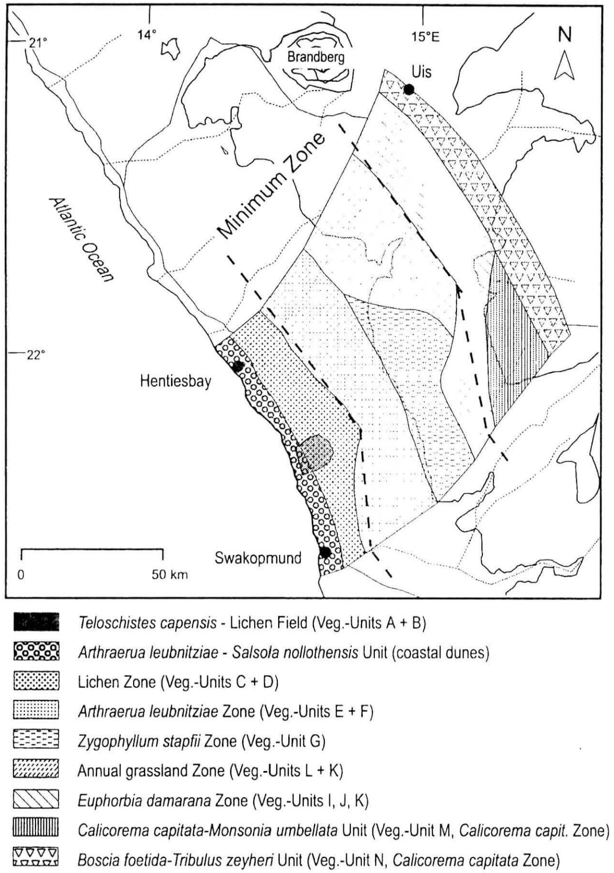

Fig. 9. Map of the major vegetation zones and Minimum Zone in the northern Central Namib Desert.

Further to the east the dominating zone is the *Calicorema capitata* Zone which partly alternates (*Calicorema capitata-Monsonia umbellata* Unit) with the *Euphorbia damara* Zone. Species composition comprises more typical savanna species though. The *Boscia foetida-Tribulus zeyeri* Unit forms the eastern border of the desert and marks the transition to savanna (Fig. 10). Canopy cover is highest with a mean of 58 % and phanerophytic species such as *Acacia reficiens* and *Boscia foetida* together with ephemeral herbs and grasses mark the typical composition of savanna type vegetation especially in years with good rainfall.

Summarising, it can be concluded that all analysed characteristics of the vegetation in the northern Central Namib Desert, i.e. the species number,

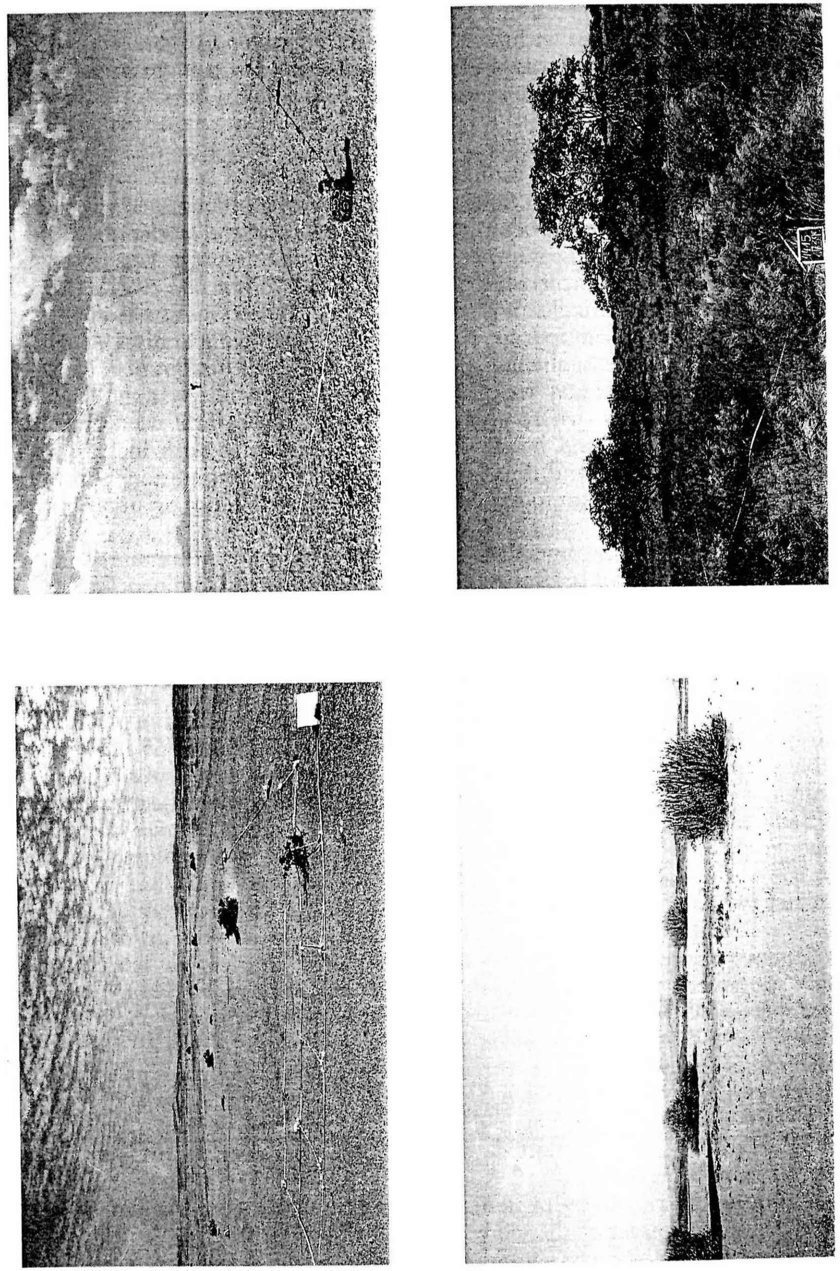

Fig. 10. Photos of major vegetation zones: Upper left: *Arthraerua leubnitziae* Zone; upper right: Minimum Zone/Annual Grassland Zone; lower left: *Euphorbia damarana* Zone; lower right: *Calicorema capitata* Zone.

total canopy cover, composition of growth forms, and the vegetation units show a significant change with respect to coastal distance and thus climatic conditions. However, towards the east of the study area a slightly greater variation especially in the composition of the vegetation occurs.

Conclusions

The northern Central Namib Desert exhibits a strong influence of climate on the vegetation. Near the coast climatic conditions are moderate with continuously mild air temperatures and high air humidity as well as a very high regularity in the occurrence of coastal fog. Additionally, coastal fog often comprises fog-drizzle. With respect to the better moisture supply species richness and canopy cover near the coast is comparatively high mainly due to the predominance of lichens. The spatial distribution of lichens in the study area very well reflects the moisture input by fog: At the coast fruticose lichens (where greatest amount of fog-drizzle was found) occur, but lichen size and height decreases continuously with increasing distance from the coast and thus less favourable climatic conditions. From a coastal distance of 20 km to the end of the fog zone (50 km) no other but crustose lichens occur.

Fog is still the main precipitation type in part of the Minimum Zone which starts at 25 km coastal distance. High/Garua fog is dominant in this part of the study area. Even though water yield by high/Garua fog is as high as by coastal fog other climatic features such as air temperature and air humidity seem to surmount this effect. The high frequency in the occurrence of east winds and thus very high air temperatures and low air humidity suggest most extreme climatic conditions for the vegetation. Annual amount of precipitation by high/Garua fog may be as high as 65 mm but weekly input is too low to sustainably develop a coherent vegetation cover. Only few chamaephytic species are adapted to these conditions. *Arthraerua leubnitziae* is such a well adapted species which is found all over the fog zone in the study area. Within the Minimum Zone of the vegetation a change in climatic conditions takes place. The area east of 50 km coastal distance is not influenced by fog anymore. Instead, the minimum in vegetation cover and species richness between 50–80 km is only due to the lack of summer rain coupled with high air temperature and low air humidity. Only sporadically chamaephytic species occur such as *Zygophyllum stapfii*. This species is present in both the foggy and non-foggy part of the Minimum Zone and has its predominance in the *Zygophyllum stapfii* Zone. Annual grasses characterising the Annual Grassland Zone only germinate after rainfall events in summer which are rare in the Minimum Zone and even more rare near the coast where the main precipitation period is winter. Therefore this zone is restricted to the middle and eastern parts of the Central Namib Desert.

With a higher regularity in rainfall amount and frequency vegetation is more dense in the east of the study area. Due to more favourable climatic conditions plant size increases and composition of the vegetation becomes

more divers. Thus more vegetation units alternate in small scale patterns and soil/bedrock conditions win a greater impact on the vegetation. Nevertheless rainfall is still highly erratic and plants have to adapt to possibly long dry periods. With a low grazing impact, stem succulent plants such as *Euphorbia damarana* as well as ephemeral species are well adapted. Additionally *Acacia* spp. and other phanerophytes are of smaller height than in the more humid inland savannas of Namibia.

It can be concluded that the homogeneous plains of the northern Central Namib Desert serve as a good model to detect and analyse the impact spatial and temporal climatic patterns have on spatial patterns of desert vegetation. The steep coast to inland gradient of major climatic elements is to a considerable extent responsible for a distinct sequence of vegetation zones, units and composition of growth forms running in a similar direction. Additionally, a minimum in species richness and total canopy cover is experienced in the midst of the desert where climatic conditions are most extreme.

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Addresses of the authors:
(please send all correspondence to the first author)
Berit Hachfeld, Norbert Jürgens, Institute of Botany, University of Cologne, Gyrhofstrasse 15, 50931 Cologne, Germany. e-mail: berit.hachfeld@uni-koeln.de