With best wishes!
B. Schieferstein
Kurt

Vegetatio **98**: 113–128, 1992.

Ecological investigations on lichen fields of the Central Namib

I. Distribution patterns and habitat conditions

B. Schieferstein & K. Loris
University of Hohenheim, Institute of Botany, PO Box 700562, D-7000 Stuttgart 70, FRG

Accepted 15.11.1991

Keywords: Biomass, Growth forms, Lichen density, Species diversity, Zonation

Abstract

Number, geographic location, extent and characteristics of lichen fields were recorded within the Central Namib fog desert. Their occurrence is restricted to stable surfaces in the near coastal belt, while percentage cover changes with exposure, elevation and distance from the coastline. Maximum coverage of 70% was found at a distance of 5 km from the coast near Wlotzkas Baken. The highest biomass rate of 400 mg/m^2 was measured here at a distance of 1 km from the coast, where *Teloschistes capensis* appears as cushion growth type. Distribution patterns on hills, riverbeds and polygon structures are described. In general, fruticose and foliose lichens dominate on SW-exposed, ocean-facing habitats. Crustose species dominate on NE-E-exposed plots.

Species composition and distribution, particularly the distribution of the fruticose species *T. capensis* (L.f.) Vain. ex Müll. Arg., were investigated in seventysix plots along twenty W-E transects in one lichen field near Wlotzkas Baken. *T. capensis* occurs in three different growth types: tuft, cushion and mat. Four zones are distinguished within the above lichen field, each dominated by a growth form indicating various influences of different climatic, geomorphic or biogenic parameters.

Introduction

The main purpose of this study was to investigate the precise occurrence and distribution of lichens in the Central Namib Desert. These lichen fields are known to be unique worldwide (Mattick 1970; Giess 1968; 1981; Wessels & Van Vuuren 1986). The ground cover by cormophytes is rather low, compared to other coastal fog deserts such as in California (Rundel 1978; Nash *et al.* 1979) and Chile (Follmann 1967; Redon & Lange 1983). The first accounts of areas with dense lichen growth were provided, among others, by Meyer (1910), Mattick (1970) and Seely (1987). Detailed ecophysiological investigations were lacking of the patchy appearance of lichen communities in connection with their micro- and macro-environmental conditions (Walter 1986). This is the first of two papers which presents the results of the investigations of the occurrence and distribution of lichens. The results of the climatic and ecophysiological investigations will be discussed in a second paper. Further basic physiological investigations were recently made by Lange *et al.* (1990; 1991).

The study area

The Namib fog desert extends as a strip 50–120 km wide for approximately 1600 km along the SW coast of Africa between the St. Nicolas River (14° 20′ S) in southern Angola and the Olifants River (32° S) in South Africa (Fig. 1).

The east of the Namib is bordered by the Escarpment, a 1200 m high mountain range which leads to the inner plateau of Namibia.

The Northern and the Southern Namib consist of large dune fields along the coast, and mountains in the interior (Fig. 1), whereas the Central Namib, between the Huab River (14° 20′ S and

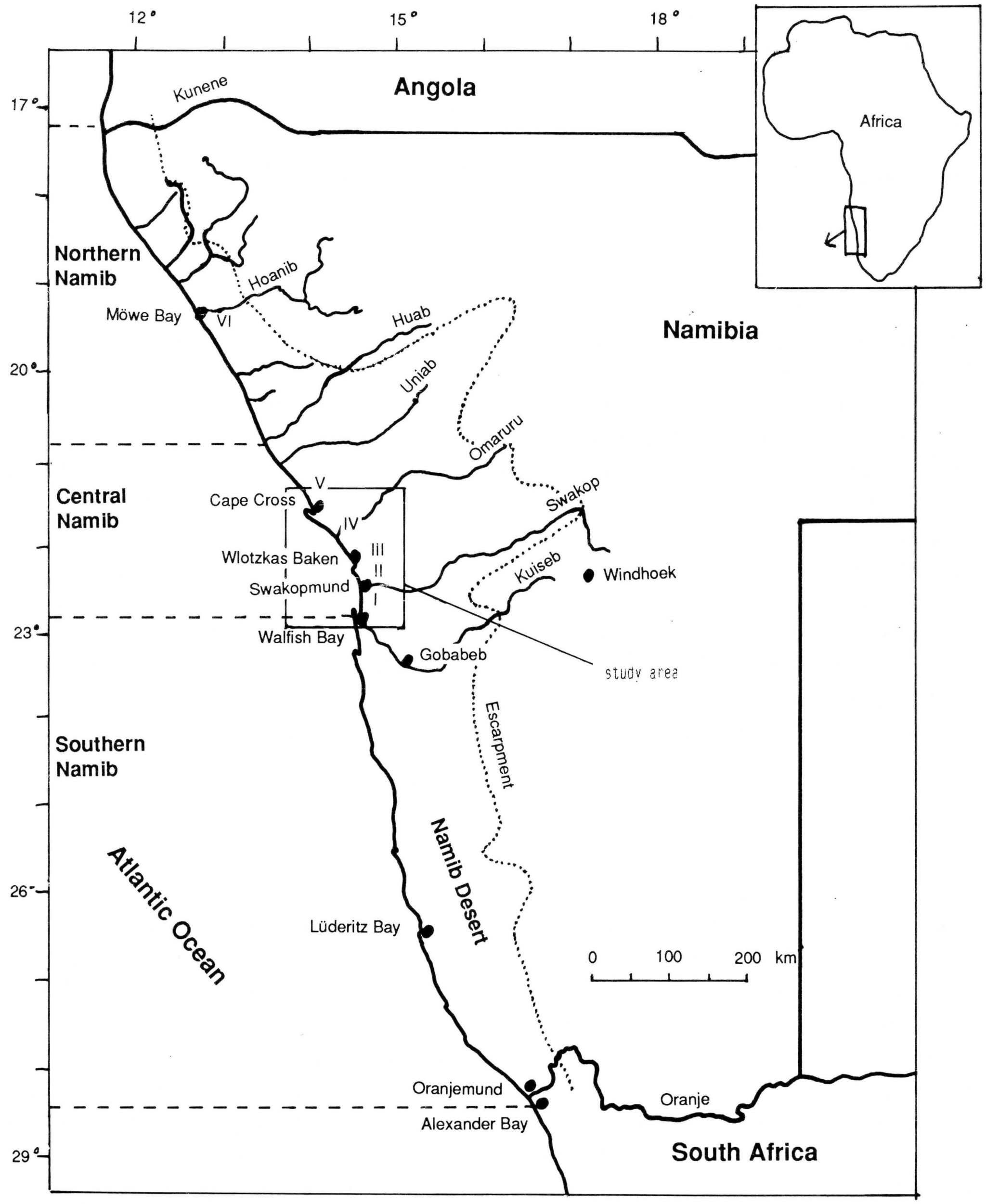

Fig. 1. The Namib Desert is divided into three areas: Northern, Central and Southern Namib. The occurrence of lichen fields is marked with numbers; the run of the Escarpment with a dotted line.

21° S) and the Kuiseb River (23° S), is a vast gravel plain without dunes and traversed by numerous dry riverbeds. The homogeneous landscape is interrupted only by a few inselbergs and rocky ridges running in a SW-NE direction as far as 40 km inland. The Central Namib is subdivided into an 'outer' and an 'inner' Namib. The outer Namib, terminating approximately 50 km from the coast, is characterized by the coastal fog belt, little or no (0–50 mm) mean annual precipitation (rain) and an annual average temperature of 18 °C. The inner Namib farther east has a mean annual summer rainfall of 50 to 100 mm and an annual average temperature of 28 °C (Walter 1986). Two main wind directions are typical for the Central Namib region. The SW-winds, coming from the sea, moisten the interior throughout the summer, while periodical strong hot and dry NE-E-winds are characteristic for the winter season.

The sparse vegetation changes within the Central Namib from the coast towards the interior. A strip of approximately 200 m width is covered immediately next to the coast with leaf succulent shrubs (e.g. *Zygophyllum stapfii* or *Psilocaulon salicornioides*). The shrub *Arthraerua leubnitziae* dominates the gravel plain further east. A more detailed description of the small Namib vegetation units is given by Jürgens (1991 in press).

Materials and methods

Survey areas and geomorphic characteristics

The position and extension of the lichen fields were mapped while driving long distance transects along the coast and a few selected inland roads. The distribution lines were compared with aereal photographs and drawn on topographic maps (1:50 000).

Variations in land elevation were measured at Wlotzkas Baken with a theodolite along W-E and N-S sections. Some data were used to construct profile drawings of selected geomorphic structures (hills, rocky ridges, riverbeds). Substrates for lichen growth usually consisted of various gravel types or sandy material. Grain size was classified according to Müller (1964). Quartz, marble and dolerite were the most prevalent minerals of the investigated area.

Lichen distribution and biomass determination

Seventysix test plots were mapped along 20 W-E and N-S transects within the dense lichen cover near Wlotzkas Baken in order to quantify apparent variations in ground cover and species composition. Each square measured one m^2 and was divided into 100 subsections (10 × 10 cm). Lichen species were identified in each subsection; unknown species were assigned a reference number. Ground cover was estimated for each species in increments of 5 to 10% and a geomorphic description added to each plot.

To determinate variations in biomass, 20 different test squares were sampled along one W-E transect. These areas were selected on the basis of ground cover, species composition and appearance of 1.) specific 'growth forms' (crustose, foliose or fruticose) and 2.) 'growth types' of the fruticose species *Teloschistes capensis* (tuft, cushion or mat). All lichen growth forms of a test plot (excluding endolithic lichens) were dried to constant weight (crustose species were scraped off from stones), then burned to ashes and weighed again. The resulting weight difference represented the organic component of the biomass per square meter.

Results

Survey areas

Lichens occur all along the coast, but densities are variable. Areas with dense lichen coverage were considered 'lichen fields' when ground cover exceeded 20% within one square meter. Between the Huab River and the Kuiseb River six lichen fields are cited (Fig. 1 and 2). Table 1 lists the taxa which generally occur in all lichen fields.

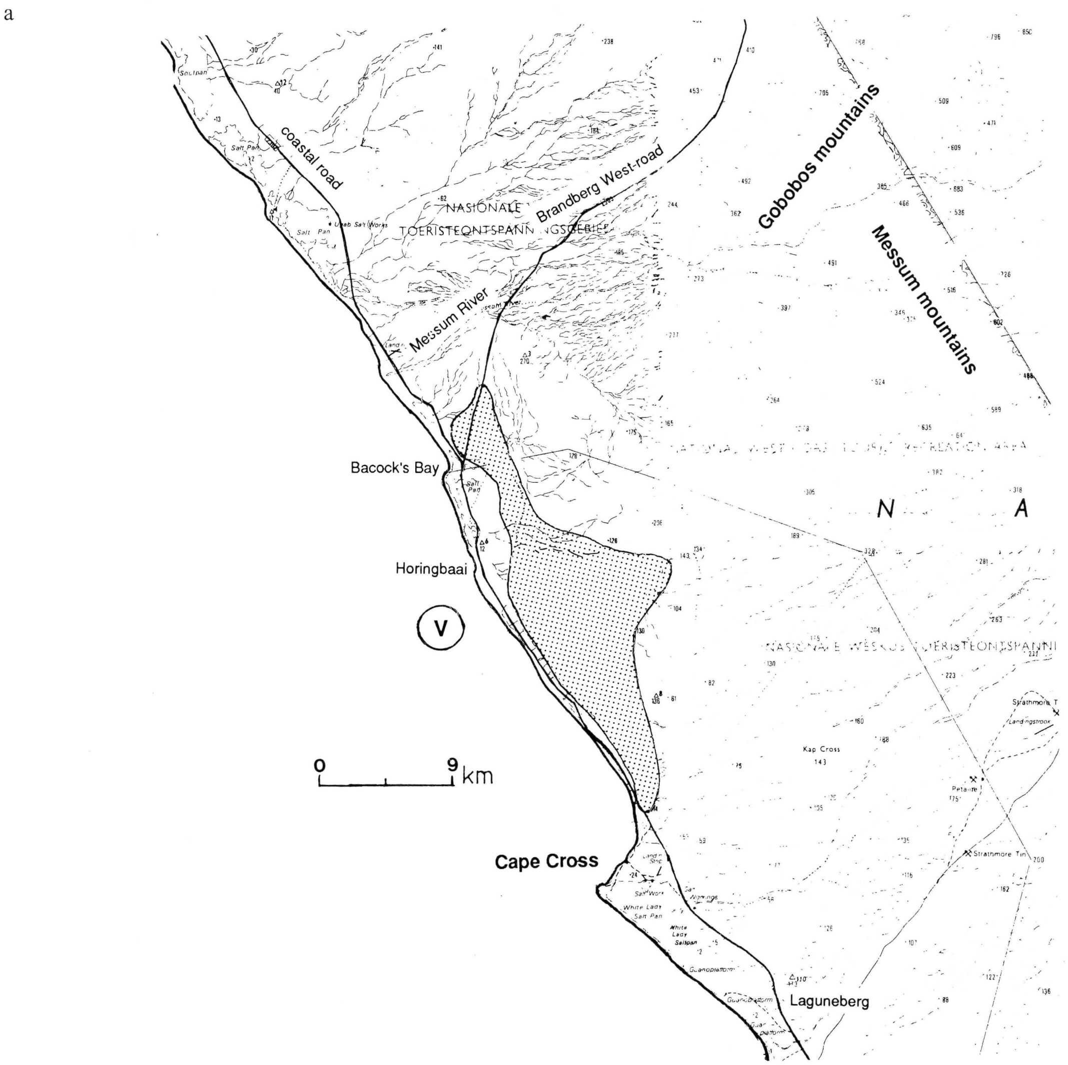

Fig. 2. (a) Location and extension of lichen field V within the Central Namib; – (b) Location and extension of lichen fields I–IV and the zonation within lichen field III.

Lichen field I. SE of Swakopmund (20° 40′ S, 14° 34′ E; Fig. 2b) an area of about 400 km^2 is covered by lichens. Crustose lichens constitute the dominant growth form. They use the quartz gravel (diameter ca. 0.5–1 cm) as substrate. In the east, approximately 40 km from the coast, lichen density sinks below 20%. Lichen occurrence is limited by rivers towards the north and south, and by linear dunes in the west.

Lichen field II. Approximately 20 km north of Swakopmund lichen field II covers an area of ca. 12 km^2 (Fig. 2b). It also is bordered by rivers in the north and in the south.

Lichen field III. The third lichen field (used for detailed vegetational and ecophysiological studies) begins 37 km north of Swakopmund and covers approximately 200 km^2 (22° 21′ S, 14° 27′ E; Fig. 2b). Beginning at 16 km from the coast the gravel plain is interspersed by rocky dolerite ridges, which face SW-NE towards the interior. In the north, lichen distribution ends in a riverbed system, while in the west salt pans and flat coastal

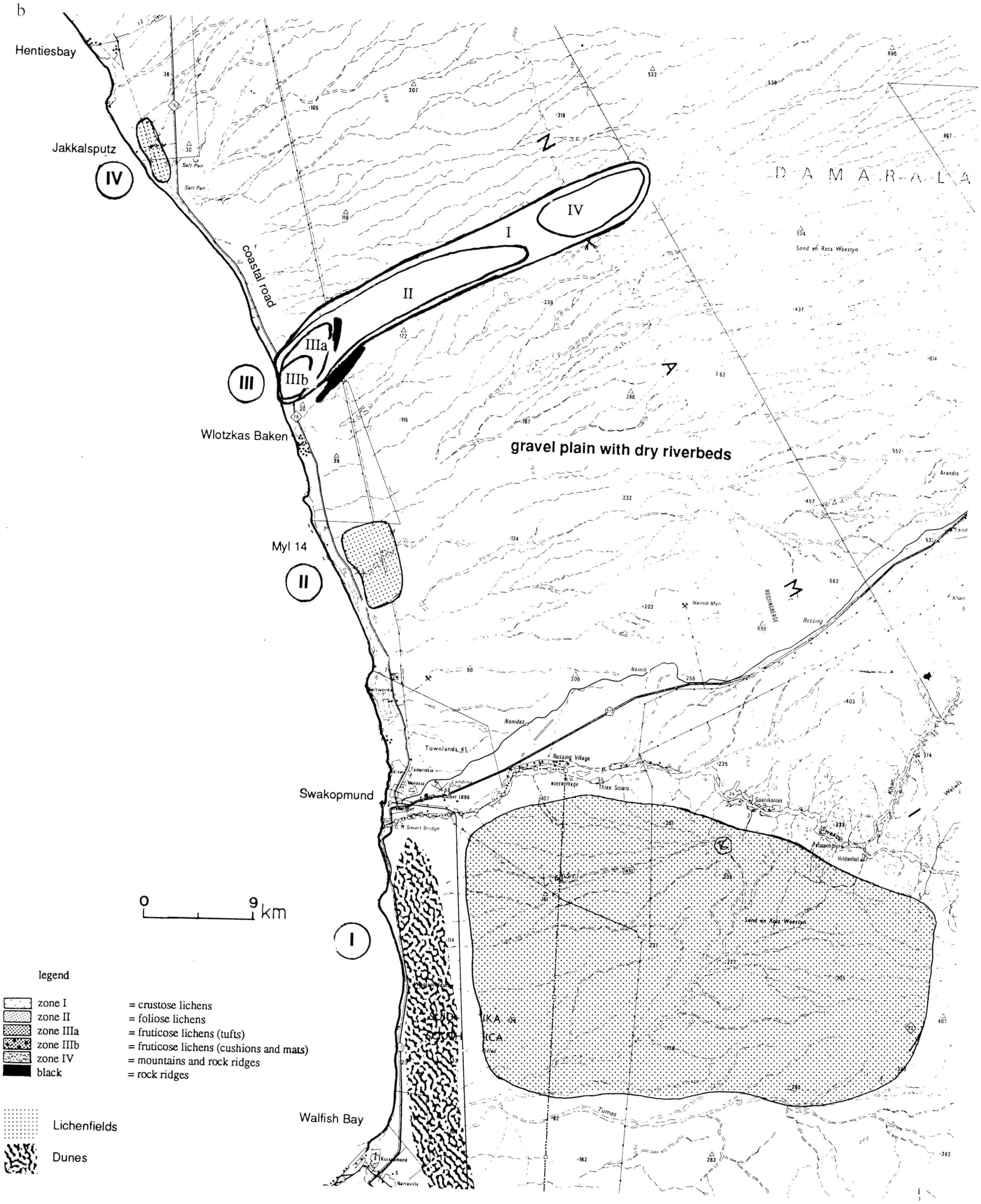

Fig. 2. Continued.

Table 1. Lichens determined in lichen field III near Wlotzkas Baken and the respective zone in which they appear.

Species	Found in zone	Literature
Acarospora spec.	I; IV	Magnusson (1933)
cf. Alectoria	III	
cf. Buellia	I; IV	
Caloplaca elegantissima (Hyl.) Zahlbr.	I	Poelt & Pelleter (1984)
C. indurata Wirth et Vézda	I	Wirth & Vézda (1975)
C. namibensis Kärnef.	I	Kärnefelt (1988)
C. volkii Wirth et Vézda	I	Wirth & Vézda (1975)
cf. Diploschistes	I; IV	
Heterodermia cf. erinacea (Ach.) Weber	III	
cf. Lecidea	I; IV	
Lecidella crystallina (Wirth et Vézda)	I	Wirth et Vézda (1975)
cf. Lepraria	I–III	
Neofuscelia namaensis (Stein et Zahlbr.) Essl.	I	Esslinger (1978)
Parmelia lecanoraceae Müll. Arg.	IV	Hale (1976)
Ramalina maculata var. tenuis Müll. Arg.	I–III	
Rinodina spec.	I	Magnusson (1947)
Santessonia hereroensis (Vain.) Follm.	III	Hale & Vobis (1978)
S. sorediata Sérusiaux et Wessels	III	Sérusiaux & Wessels (1984)
Teloschistes capensis (L.f.) Vain. ex Müll. Arg.	III	Almborn (1989)
T. chrysophthalmus (L.) Th. Fr.	IV	Almborn (1989)
Trichoramalina melanothrix (Laur.) Rundel et Bowler	I; III	Rundel & Bowler (1974)
Xanthomaculina convoluta (Hue) Hale	I	Hale (1985)
X. hottentotta (Ach.) Hale	IV	Hale (1985)
Xanthoparmelia serusiauxii Hale	IV	Hale (1986)
X. walteri Knox	II	Knox (1983)
Xanthoria turbinata Vain.	II–IV	Hillmann (1922)
X. flammea (L.f.) Hillm.	IV	v.d. Bijl (1933)

dunes, with a shrub vegetation, from the border. In the south (close to the coast) a 3 to 10 cm thick layer of sand, deposited by the local seasonal East wind, appears to hinder further lichen colonisation.

Lichen field IV. 6 km south of Henties Bay (22° 7′ S, 14° 17′ E; Fig. 2b) lichen field IV covers an area of 10 km^2. Again rivers form borders, as well as a salt pan in the west.

Lichen field V. This lichen field begins ca. 5 km north of Cape Cross (21° 35′ S; 13° 56′ E; Fig. 2a) and extends northwards over 25 km to the point where the 'Brandberg West-road' forks east, covering approximately 300 km^2. The eastern distribution line borders the N-S oriented western range of the Messum mountains, which is situated 15 km from the coast. A 2 km wide zone situated about 16 km north of Cape Cross, is covered by windborne sand, apparently suppressing further colonisation by lichens (compare to the southern distribution line of lichen field III).

Lichen field VI. The most northerly of the lichen fields of the Central Namib lies south of the Huab River (20° S) in the Skeleton Coast National Park (Fig. 1), covering 9 km^2. The factors limiting lichen extension are the same as in lichen field IV.

Three growth types of Teloschistes capensis

Lichen fields III and V serve as examples for three different growth types of *T. capensis* (tuft, cushion and mat). Distribution of *T. capensis* extends from Cape Town to Angola, however different growth types appear which often grow closely adjacent to each other only in lichen field III and V.

Lichen tufts

Clusters of *T. capensis* consist of individual thalli that have grown together as a tuft (Fig. 3), and are up to 5 cm tall with a diameter of up to 4 cm.

Lichen cushions

T. capensis cushions consist of numerous thalli growing in close association with one another. Covering an area of 10 to 30 cm in diameter (Fig. 3), they may reach up to 10 cm in height and occur on the plain as well as on hill slopes. Thalli on the sea-facing SW-exposed side are usually 1 to 3 cm longer than on the opposite side. Due to the alternating hot and sand blowing East wind or moist North or SW winds the cushions may be covered with sand or turned over. The part covered underneath then usually dies. Only a few thalli grow on the SW-facing side of their new form.

Lichen mats

T. capensis mats are an amalgamation of many cushions which have grown together ribbon-like or in polygon or circle form. They originate from tufts which have accumulated around low lying cormophytes. In many cases those mats span the surface like a net, reaching diameters of 1 to 2 meters.

The process by which different growth types are able to develop close to each other without transitional stages, was not known at the beginning of this research. Observation and investigation illustrated that besides climatic and mechanical parameters, biogenic reasons determine the distribution of the growth types. Dead remains of cormophytes were found underneath ninety percent of a hundred investigated lichen cushions (Fig. 4). Usually they belong to species of the families *Aizoaceae* or *Mesembryanthemaceae*, which weather quickly when they are dead and uncovered. These dead remains indicate that the cormophytes had still been alive when colonization by lichens started. On days with a strong East wind lichens, mainly tufts, are torn from their anchoring points, removed, and get trapped on the cormophytes. This leads to complete overgrowth by lichens. The diameter of the cushions and mats depends on the diameter of the cormophyte.

Fig. 3. Tuft (1) and cushion (2) growth type of *Teloschistes capensis*.

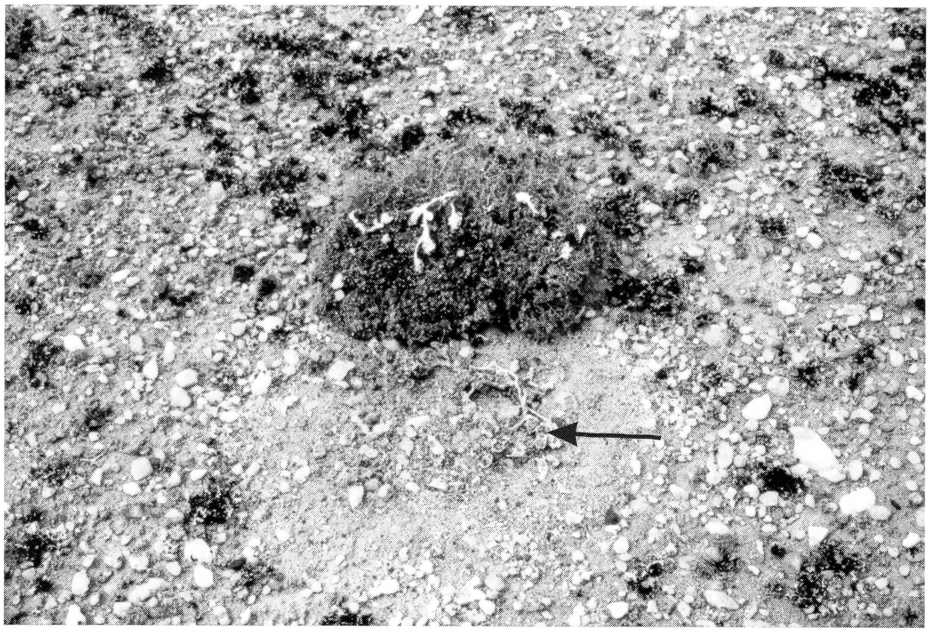

Fig. 4. Lichen cushion with dead remains of *Mesembryanthemum cryptanthum* underneath.

Two additional factors are decisive for cushion development. Firstly, lichen thalli, attached and compacted by wind to upright parts of dead plants, absorb more moisture, especially fog (see part II). When thick patches of lichens develop, they hold back moisture much longer and dehydrate later in the morning than tufts. The time span for photosynthesis is longer for the lichen thalli within cushions. Secondly, the tight packing of the cushions makes them less susceptible to being blown off by wind.

Lichen and biomass distribution at lichen field III

Figure 5a includes a graph with data of the total ground cover (expressed as percentage per square meter) of all lichen species from different mapping areas along a W-E transect from the coast towards 25 km inland (Table 1, s.a. Fig. 2b). The highest ground cover of 70% is found at 5 km from the coast. The two lowest cover levels (between 10 to 15%) were measured near the coastline and beyond 30 km from the coast. Low rates of ground cover seem to be correlated with the occurrence of noncrustaceous soils and/or with NE-exposed areas. High rates of ground cover are usually found at SW-exposed plots.

The various growth forms have their density optima at different distance from the coast and height above sea level. Up to 1 km and beyond 15 km from the coast, crustose lichens dominate; between 1 to 15 km from the coast foliose lichens, mainly *Xanthoparmelia walteri*, have higher coverage. From 1.5 to 4 km from the coast fruticose lichens, especially *Teloschistes capensis*, grow on crustose and foliose lichens.

Species diversity (= number of species/m^2) remains nearly constant along the transect. On the average, 12 species per square were identified. A few species are restricted to the interior (e.g., *Xanthomaculina hottentotta* and *Teloschistes chrysophthalmus*), while others, like *Combea mollusca*, are confined to the coastal belt.

Biomass distribution along a W-E transect is illustrated in Figure 5b. The highest biomass (mean dry weight of ca. 400 g/m^2) was measured 1 km from the coast where *T. capensis* cushions occur with high ground cover (zone IIIb). Biomass diminishes from this point in all directions,

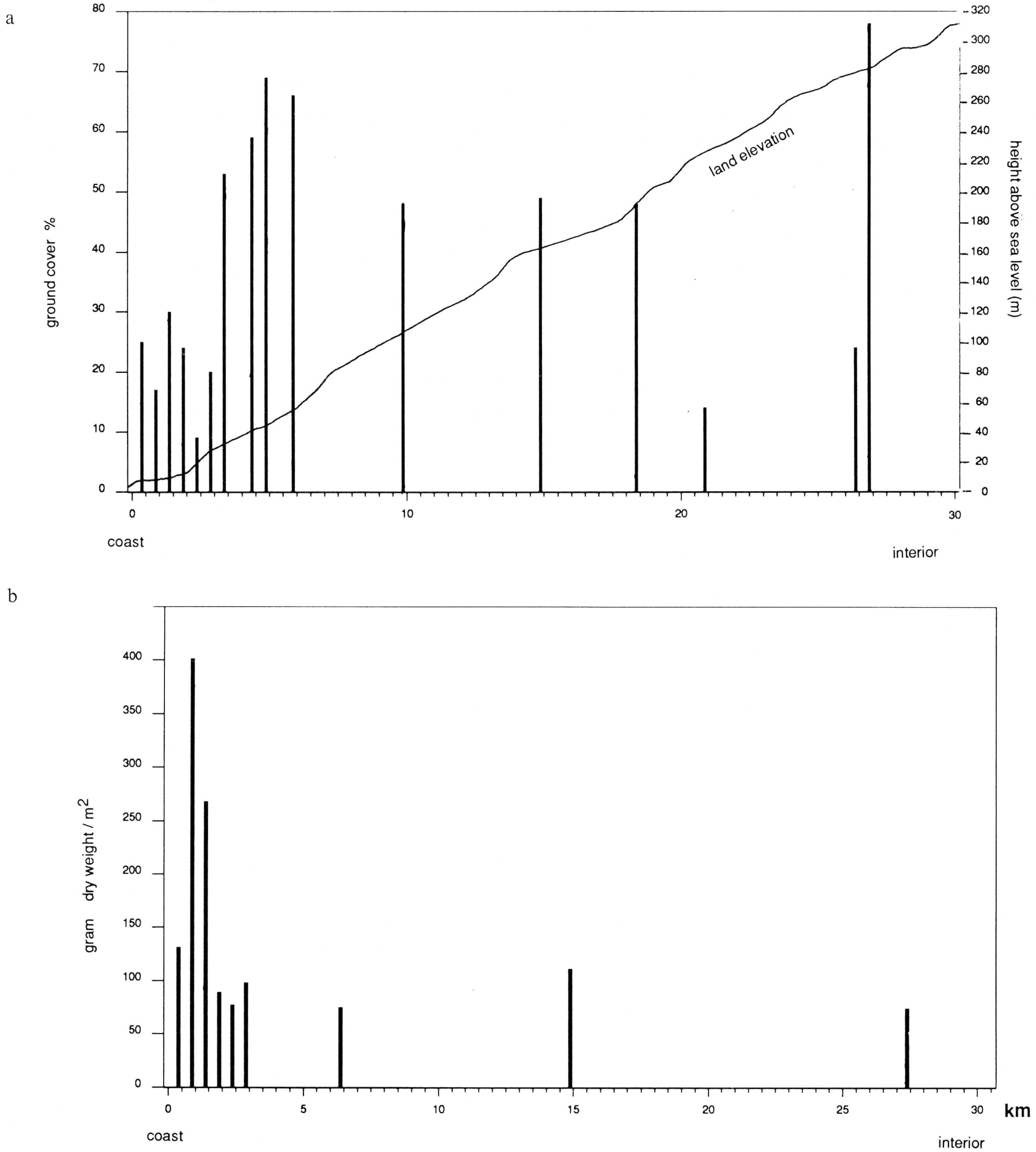

Fig. 5. (a) Total ground cover of lichens along a W–E transect from the coast towards the interior of lichen field III together with the respective land elevation; – (b) Biomass distribution along the W-E transect.

until approximately 15 km from the coast, where ground cover rises as well as biomass (ca. 48% ground cover, mainly crustose and fruticose lichens; ca. 110 g/m^2 biomass).

Zonation

In lichen fields, especially where *Teloschistes capensis* cushions occur (lichen fields III and V), a distinct zonation exists. In lichen field III for example four zones appear (Fig. 2b) and each zone is characterized by the dominance of a growth form, a growth type or a lichen species. Table 1 lists taxa which it was possible to identify, the literature used for identification, and the zones in which they appear with preference.

Zone I:. Crustose lichens: Especially in the outer area of the lichen field mainly crustose Caloplacas dominate in this zone (coverage ca. 20%).

Zone II:. Foliose lichens: The highest amount of ground cover in zone II (30%) is determined by foliose lichens, particularly *Xanthoparmelia walteri*. Zone II extends from 0.5 to 16 km from the coast.

Zone III:. Fruticose lichens: *Teloschistes capensis* with its orange colour determines the aspect of this zone, but does not always reach the highest ground cover within the mapped plots of the zone. This visible dominance is caused by their vertical growth in contrast to foliose and crustose lichens, which grow close to the surface. Two subzones can be recognized based on the distribution of different growth types of *T. capensis* (see before).

Zone IIIa:. is dominated by *T. capensis* as tufts, and

Zone IIIb:. where cushion and mat type of *T. capensis* mainly occur. This area covers approximately 6 km^2 in which the total ground cover by cushions varies because of different densities at different expositions to environmental factors (SW-exposed slopes – up to 80%; NE-exposed plots – up to 30%).

Zone IV:. Mountain and Inland zone: Zone IV is confined to slopes of rock ridges and mountains of the interior and characterized by the appearance of the species *Xanthomaculina hottentotta*, the center of whose thallus is anchored to the rocks. Thus this species has a higher stability against the strong, sandblowing East wind than, for example, the thin lobed species *Teloschistes capensis*. Further characteristic species of this zone are listed in Table 1. *T. chrysophthalmus* occurs as an epiphyte, restricted to SW-exposed branches of *Sarcocaulon sp.* shrubs or *Acacia albida* trees. Sometimes *Xanthoria turbinata* and *X. flammea* grow as epiphytes as well. They were observed not only on *Lycium sp.* or *Zygophyllum sp.* shrubs in the interior, but also on *Arthraerua leubnitziae* plants at the coast. The reason for this specific growth on a few selected shrub species is not yet known.

In the lichen fields I, II and VI the zones IIIb and IV are missing, because *T. capensis* does not occur as cushion or mat growth types. These lichen fields do not have rocky habitats which offer the necessary substrate for *X. hottentotta*.

The different growth forms and growth types may grow in several layers on top of one another. Usually foliose lichens use crustose ones as a substrate and fruticose species may grow on crustose and foliose species.

Lichen and biomass distribution in selected habitats

Within each zone slight changes of the geomorphic structure may induce deviations from mean ground cover.

Hills and rock ridges

Hills with mean heights between 5 to 8 m, or rock ridges in the interior with heights between 20 to 40 m, belong to the most elevated geomorphic structures within lichen field III. A scheme of a hill, in NE-SW cross-section, is depicted in Figure 6a. It rises up at 2.3 km from the coast in lichen field III. *T. capensis* cushions are limited to the SW-exposed slope, facing towards the sea. Their occurrence results in the highest ground cover of 50% compared to the other slopes (Fig. 6b). The extension of the cushions towards the top of the hill stops abruptly at the edge of the plateau. Whereas there are nearly no fruticose lichens (11%) on top of the hill, foliose lichens are represented with 13% ground cover. Both foliose and fruticose species occupy only a tiny part of the total ground cover of the NE-exposed slope, where crustose species dominate with a mean ground cover of 17%.

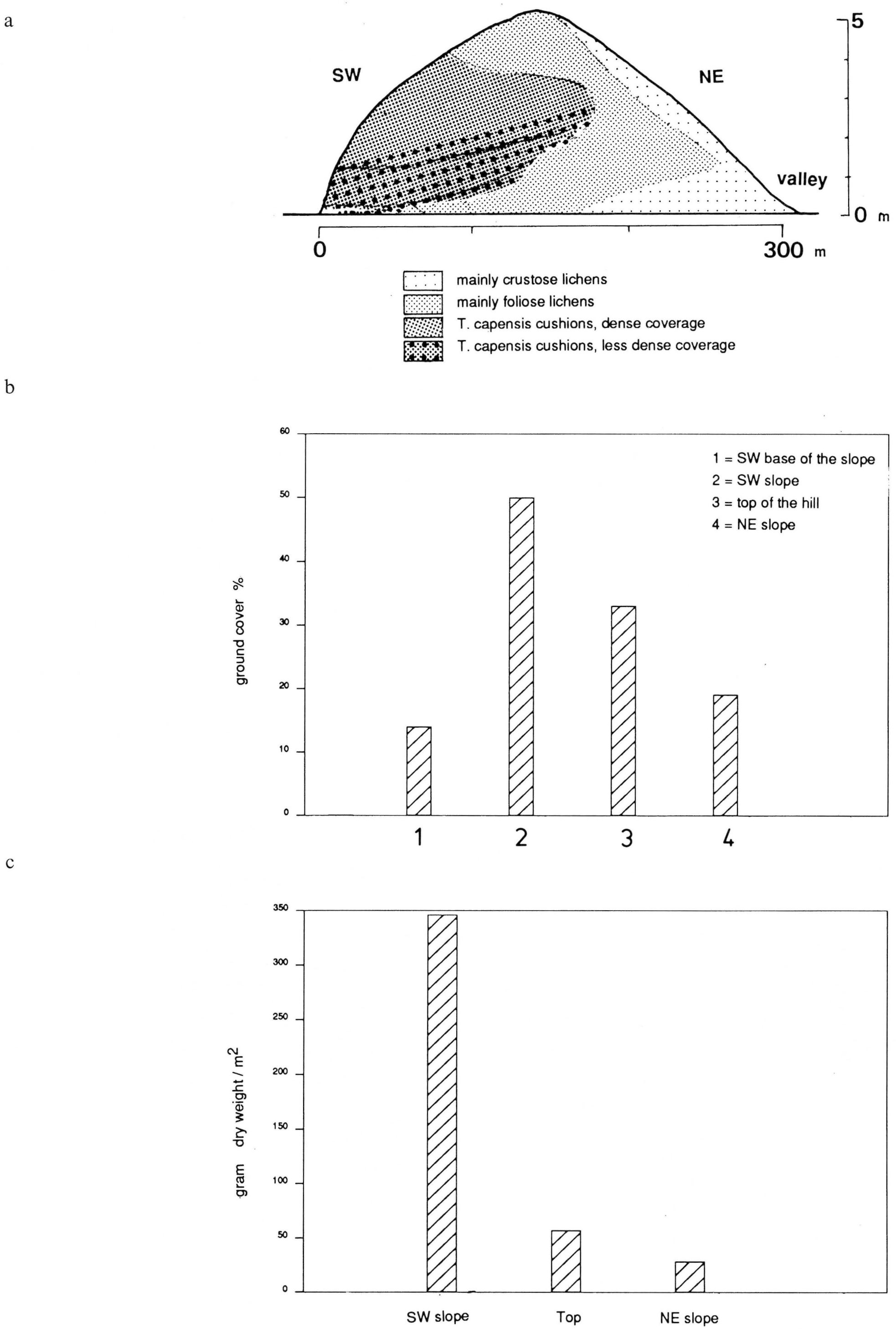

Fig. 6. (a) Profile of a hill from lichen field III with typical distribution of lichen growth forms at different expositions; – (b) Total ground cover in percentage at different slopes of the hill; – (c) Biomass distribution on different exposed slopes of the hill.

The distribution of biomass on different exposures corresponds to the above variation of lichen growth. The SW-exposed slope has the highest biomass (ca. 350 g/m^2; Fig. 6c). On top of the hill the biomass decreases to ca. 60 g/m^2. The lowest biomass was measured at the NE-facing slope with ca. 30 g/m^2.

Boulders

Lichen growth on rocks is different at the coast in comparison to the interior of lichen field III. Whereas the sandblowing and hot East wind polishes the E-facing stones, shrubs and even lichens (Fig. 7), this effect tempers towards the coast, where it is possible for *Caloplaca elegantissima* to grow on NE-exposed sides of rocks in particular.

Dry riverbeds

A similar growth pattern is found at narrow and broad dry riverbeds. Usually the SW-exposed riverside presents a high ground cover of ca. 65%. The riverbed can be subdivided into upper stabilized river banks (lichen growth up to 50%) and lower channels (without lichens). The channels contain unstable substrates as a result of drying and moistening caused by the effects of fog or dew. The N- or NE-facing riverside are usually covered between 5 to 20%. Lichens grow between shrubs in the riverbed if the mean distance between the shrubs is at least as big as the mean diameter of the shrub itself. Wherever shrubs had died plain round spots are left behind (Fig. 8). The time span for recolonization by lichens is not yet known.

Polygon structures

With a diameter between 15 to 20 cm (Fig. 9) the polygon structures in lichen field III near Wlotzkas Baken are the smallest ones observed in the Namib desert until now (Schieferstein 1989). They appear in depressions, on the base of hills, or on riverbanks. Comparable to salt pans, the upper soil layer in the area of polygons expands and shrinks with varying supply or absence of moisture.

A polygon can be divided into a central pocket-sized depression (approximately 10 to 15 cm deep) filled with sandy material, which is sur-

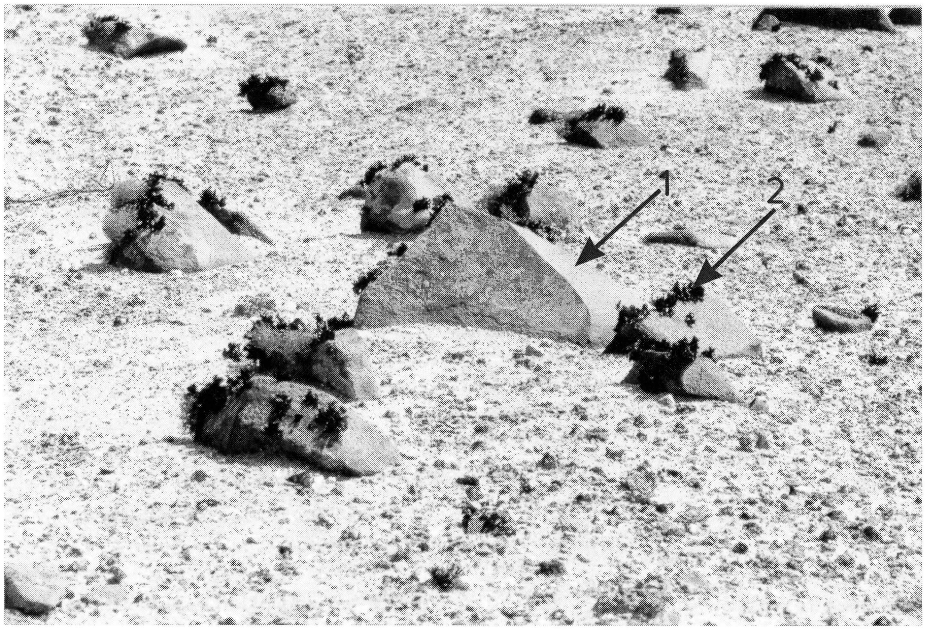

Fig. 7. Polished rocks by sandblowing East wind (1) in the interior of lichen field III where *Xanthomaculina hottentotta* (2) dominates.

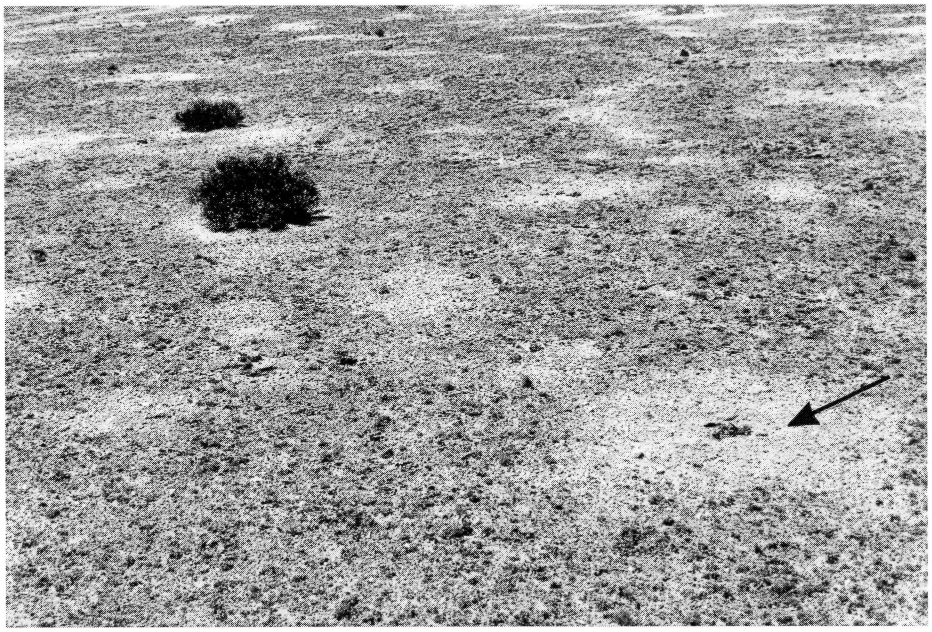

Fig. 8. Bare spots remain where shrubs used to grow.

Fig. 9. Polygon structures near Wlotzkas Baken in the Central Namib.

rounded by a gypsum layer rising up around the sand to the surface. At the deepest point of depressions, polygons are very soft and sandy with almost no lichens. The gypsum crust increases with elevation and leads to a more stable surface and denser lichen cover. The highest landmarks, where polygons appear, consist of just one gypsum layer and the polygons can hardly be recognized.

Succession of lichen growth follows the varying stability of the soil and ends when the rim of each polygon is covered with fruticose lichens.

Discussion

Besler (1972) and Walter (1986) suggested a connection between lichen distribution, input of moisture, and stability of the substrate. A selection of limiting and promoting factors for lichen distribution have been discussed in this paper.

The restriction of the unique and rich lichen fields to the Outer Central Namib is favoured by the lack of dunes and the existence of a vast, and for the most parts stable, gravel plain in connection with a quiet regular supply of moisture.

The distribution limits of a single lichen field are determined by the dominance of climatic, geomporphic, biogenic or physiological parameters. Hot and sand-transporting easterly winds determine the southern limit of lichen field III and the northern limit of lichen field V by detaching the lichens from their anchoring points or covering them with sand. In parts of the interior the winds are channelled by gaps in the mountains, which stretch in a N-S direction. The same mountains are covered by lichens on their lee sides where shelters have formed against the easterly winds (lichen field V). Other possible geormorphological structures limiting lichen distribution are dry river beds (lichen field I, II, III; towards the north and/or south) and salt pans (lichen field III, IV, VI; towards the west). The eastern distribution limits might be due to other climatic factors, such as high temperature and less humidity throughout the day (see following paper).

The distribution limits for the different species, growth forms and growth types within one lichen field are dependent on distance from the coast, elevation, climatic gradients, wind and sand force, substrate and physiological adaptation. Investigation of the zonation within each field gives hints of the determining factors for each species. The lack of dense cover by fruticose species, for example in lichen field I, is caused by the local easterly winds, which are not restrained by any geomorphologic barrier in the interior. Wind in connection with the occurrence of cormophytes, leads to the clear boundaries of zone IIIb where cushion and mat growth types of *T. capensis* dominate (lichen field III, V). As cormophytes need heavy rainfalls to germinate, it could be maintained that rainfall has an indirect influence on the occurrence of cushions. In lichen field V a steep climatic gradient due to the N-S oriented mountain range in the interior might cause the compression of the four zones in the W-E direction.

We have observed the same limiting factors for lichen distribution in other lichen fields outside the study area. At Alexander Bay (28° 40′ S, 16° 30′ E; Fig. 1), a lichen field in the Southern Namib already described by Jürgens & Niebel (1991), the sand-polishing effect of easterly winds again limits extension of lichens towards the north and south. Species are abundant only on the lee side of hills. Succulents and lichens growing as epiphytes are more frequent here than in the Central Namib (Jürgens 1986), and species diversity and biomass are higher, although no cushions were found.

Within the survey area the six lichen fields are so close to each other that the whole Central Namib might be considered as one lichen field with a zonation comparable to a single lichen field. From north to south, towards the center of the Central Namib, density levels and biomass increase to a maximum near Wlotzkas Baken and Cape Cross, where all zones are present.

Studies about diversity and structure of desert lichen communities and vascular plants from other coastal fog deserts, like in the Atacama or in the Negev Desert, show similarities to the structures investigated in the Namib. There are no lichen fields described from the other coastal fog deserts, but zonation of different growth forms and species in connection with increase of height above sea-level and input of moisture was investigated in Chile (Rundel & Mahu 1976; Redon & Lange 1983). Lichens cover the phanerophytes of the different zones at different heights as epiphytic vegetation. This is similar to the growth pattern on succulents which was described by Jürgens (1991) for the lichen field in the Southern Namib.

Kappen *et al.* (1980) describe a remarkable variation in density and species richness on different exposures in the highlands of the Negev desert. In opposite to the Namib, in the northern hemisphere the NE exposed slopes are covered densely with lichens which is caused by higher isolation rates and input of moisture than on SW exposures.

Further comparative investigations between all lichen fields of the Namib are necessary for the understanding of their specific distribution patterns and habitat conditions.

Acknowledgements

We are grateful to the H. and E. Walter foundation for funding this study by the Schimper Stipendium. We would like to thank both Dr. M. Seely, the director of DERU (Desert Ecological Research Unit), and Nature Conservation of Swakopmund for technical help in the field. With the support of Prof. Dr. B. Frenzel it was possible to complete this study at the Institute of Botany (University of Hohenheim). Dr. D. Wessels (University Sovenga) assisted with identification of lichens. We would also like to thank Dr. N. Jürgens, Barry Emslie, L. Wadsworth Moll and U. Kohla for revising the manuscript.

This paper is dedicated to Dr. E. Walter who died in 1992.

References

Almborn, O. 1989. Revision of the lichen genus Teloschistes in central and southern Africa. Nord. J. Bot. – Section of lichenology 8(5): 521–537.

Besler, H. 1972. Klimaverhältnisse und klimageomorphologische Zonierung der zentralen Namib (Südwestafrika). Stutt. Geogr. Stud. 83: 211 p.

Esslinger, T. L. 1978. A new status for the brown Parmeliae. Mycotaxon 7: 45–54.

Follmann, G. 1967. Die Flechtenflora der nordchilenischen Nebeloase Cerro Moreno. Nova Hedwigia 14: 215–281.

Giess, W. 1968. A short report on the vegetation of the Namib coastal area from Swakopmund to Cape Frio. Dinteria 1: 13–30.

Giess, W. 1981. Die in der Zentralen Namib von Südwestafrika/Namibia festgestellten Pflanzenarten und ihre Biotope. Dinteria 15: 13–72.

Hale, M. E. 1976. A monograph of the lichen genus Pseudoparmelia Lynge (Parmeliaceae). Smithson. Contrib. Bot. 31: 35–37.

Hale, M. E. 1985. Xanthomaculina (Hale) a new lichen genus in the Parmeliaceae (Ascomycotina). Lichenologist 17(3): 255–265.

Hale, M. E. 1986. New species of the lichen genus Xanthoparmelia from Southern Africa (Ascomycotina: Parmeliaceae). Mycotaxon 27: 563–610.

Halel, M. E. & Vobis, G. 1978. Santessonia, a new lichen genus from South West Africa. Afr. Bot. Notiser 131: 1–5.

Hillmann, J. 1922. Übersicht über die Arten der Flechtengattung Xanthoria (Th. FR.) Arn. Hedwigia 63: 198–208.

Jürgens, N. 1986. Untersuchungen zur Ökologie sukkulenter Pflanzen des südlichen Afrika. Mitt. Inst. Allg. Bot. Hamburg 21: 139–365.

Jürgens, N. & Niebel, A. 1991. A lichen field near Alexander Bay. Veld & Flora 77(1): 24–26.

Kappen, L., Lange, O. L., Schulze, E.-D., Buschbom, U. & Evenari, M. 1980. Ecophysiological Investigations on Lichens of the Negev Desert. VII. The Influence of the Habitat Exposure on Dew Imbibition and Photosynthetic Productivity. Flora 169: 216–229.

Kärnefelt, I. 1988. Two closely related species of Caloplaca (Teloschistaceae, Lichenes) from the Namib Desert. Bothalia 18: 51–56.

Knox, D. M. E. 1983. New Xanthoparmeliae (Lichenes) from southern and central Africa. J. S. Afr. Bot. 49(2): 143–159.

Lange, O. L., Meyer, A., Zellner, H., Ullmann, I. & Wessels, D. C. J. 1990. Eight days in the life of a desert lichen: water relations and photosynthesis of Teloschistes capensis in the coastal fog zone of the Namib desert. Madoqua 17(1): 17–30.

Lange, O. L., Meyer, A., Ullmann, I. & Zellner, H. 1991. Mikroklima, Wassergehalt und Photosynthese von Flechten in der küstennahen Nebelzone der Namib-Wüste: Messungen während der herbstlichen Witterungsperiode. Flora 185: 233–266.

Magnusson, A. H. 1933. Supplement to the Monograph of the Genus Acarospora. Ann. Cryptog. Exotique 6: 13–48.

Magnusson, A. H. 1947. Studies in Non-Saxicolous Species of Rinodina. Acta Horti Gotoburgensis 17: 207–214.

Mattick, F. 1970. Flechtenbestände der Nebelwüste und Wanderflechten der Namib. Namib und Meer 1: 35–43.

Meyer, H. 1910. Das deutsche Kolonialreich. Eine Länderkunde der deutschen Schutzgebiete. Bd. II. Bibliograph. Inst., Leipzig u. Wien.

Müller, G. 1964. Sediment-Petrologie I; Methoden der Sediment-Untersuchung. Stuttgart.

Nash, T. H., Nebeker, G. T., Moser, T. J. & Reeves, T. 1979.

Lichen vegetation gradients in relation to the Pacific coast of Baja California: the maritime influence. Madronjo 26: 149–163.

Poelt, J. 1969. Bestimmungsschlüssel europäischer Flechten. Cramer, Lehre/Vaduz.

Poelt, J. & Pelleter, U. 1984. Zwergstrauchartige Arten der Flechtengattung Caloplaca. Pl. Syst. Evol. 148: 51–88.

Redon, J. & Lange, O. L. 1983. Epiphytische Flechten im Bereich der chilenischen 'Nebeloase' (Fray Jorge) I. Vegetationskundliche Gliederung und Standortsbedingungen. Flora 174: 213–243.

Rundel, P. W. 1978. Ecological Relationships of Desert Fog Zone Lichens. The Bryologist 81(2): 277–293.

Rundel, P. W. & Bowler, P. A. 1974. The lichen genus Trichormalina. Bryologist. 77: 188–194.

Rundel, P. W. & Mahu, M. 1976. Community Structure and Diversity in a Coastal Fog Desert in Northern Chile. Flora 165: 493–505.

Schieferstein, B. 1989. Ökologische Untersuchungen an den Flechtenfeldern der Namib Nebelwüste. Diplomarbeit Univ. Stuttgart-Hohenheim. 180p.

Seely, M. 1987. The Namib. Windhoek. 104p.

Serusiaux, E. & Wessels, D. C. 1984. Santessonia (Lecanorales, Buelliaceae) in the Namib desert (SWA). Mycotaxon 19: 479–502.

van der Bijl, P. A. 1933. I. Fam. Roccellaceae; II. Fam. Teloschistaceae. Annal. Univ. Stellenbosch Jaarg. XI, Reeks A.

Walter, H. 1986. The Namib Desert. In: Evenari, M., Noy-Meir, J., Goodall, D. W. Hot Desert and Arid Shrubs. Elsevier Science Publishers B. V. Amsterdam. 245–282.

Wessels, D. C. J. & van Vuuren, D. R. J. 1986. Landsat imagery – its possible use in mapping the distribution of major lichen communities in the Namib desert, SWA. Madoqua 14(4): 369–373.

Wirth, V. 1980. Flechtenflora. Stuttgart. 552p.

Wirth, V. & Vézda, A. 1975. Drei neue Flechtenarten aus SWA. Stuttg. Beitr. Naturkd. Ser. A. 284: 1–4.