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# Lichen distribution along an ocean-inland transect in the fog zone of the Central Namib

VOLKMAR WIRTH\*, JUTTA MÜLLER, MICHAEL PFIZ, KURT LORIS & MANFRED KÜPPERS

**Summary:** The lichen flora on gravel plains in the Namib-Desert fog zone north of Swakopmund in Namibia was investigated at 25 sites along a transect extending from the coast 40 km inland. In total, 42 lichen species were found, which were classified into four groups with different distribution patterns, namely: (1) *Caloplaca testudinea* group comprising *C. testudinea*, *C. namibensis*, *C. volkii*, *Buellia incrustans*, *Lecidella crystallina*, *Xanthoparmelia walteri*, and *X. namibiensis* (within the taxonomical group of *X. dregeana* s.l.) present both inland and along the coast, (2) *Teloschistes* group comprising *Teloschistes capensis*, *Ramalina* spp. and *Xanthoparmelia tentaculina* restricted to the coast, (3) *Caloplaca rubelliana* group consisting of *C. rubelliana*, *Buellia peregrina*, *B. stellulata*, *Lecidella placodina*, *Xanthoparmelia incomposita* and *Acarospora* species common inland but absent from the coast, and (4) *Xanthoparmelia serusiauxii* group comprising *X. serusiauxii*, *X. evernica*, *X. lapidula* occupying a zone even further inland. Both climatic and mechanical factors affect these lichen distribution patterns.



Photo 1: *Xanthoparmelia tentaculina* of distribution type 2. Photo: V. Wirth.

## Introduction

An astonishing phenomenon of coastal subtropical deserts, especially the hyperarid Atacama and Namib, is their exceptionally high biodiversity. Frequent fog and dew precipitation facilitates the survival of flora and fauna in the coastal parts of these deserts despite the low rainfall. Fog precipitation is most easily utilised by lichens, which therefore play an important ecological role in these so-called “fog deserts”.

In the Namib Desert, lichens occur so frequently that they dominate the landscape. Mattick (1970) defined such areas as “lichen fields”, eight of which occur between the Kuiseb and Ugab rivers (Schieferstein & Loris 1992). Lichen fields dominated by the fruticose lichen *Teloschistes capensis* are well known for their orange coloured mats of high biomass, which seemingly cover the soil surface and they are consequently described as terricolous (Lalley & Vlies 2005) even though most of these and other co-occurring lichen species are indeed saxicolous,

depending on gravel substrates for their establishment.

Previous studies of the coastal lichen fields in the Namib Desert between Swakopmund and Ugabmond have shown that the lichen species are not distributed homogeneously (Walter 1937, Giess 1981). The conspicuous *Teloschistes capensis*, which is dominant along the coast, declines in density inland with a somewhat similar pattern displayed by the greenish foliose lichen *Xanthoparmelia walteri*. In more inland areas, crustose lichens and those with adnate foliose thalli such as *Xanthoparmelia incomposita* and *serusiauxii* are more common. These diverse patterns of lichen species distribution have been attributed to a decline in the amount and frequency of fog precipitation, which is necessary for intermittent lichen thallus hydration with increasing distance from the coast (Walter & Breckle 1991: 282, Lange et al. 1991).

## Materials and methods

The study area comprised a transect aligned almost perpendicular to the coastline (Fig. 1) extending from the coast at Wlotzkas Baken, which is 40 km north of Swakopmund (22°22'17" S 14°25'50" E), to a point approximately 40 km inland (22°08'35" S 14°42'16" E). Twenty-five evenly spaced sampling sites were established along this transect when suitable habitats allowed. Each selected site comprised a uniform gravel plain composed of more or less rounded, partly embedded, pebbles of similar size covering between 40% and 60% of the soil surface. At each site, lichen species composition and abundance were determined in 10 x 0.1 m<sup>2</sup> fully randomised plots, each subdivided into 10 x 0.01 m<sup>2</sup> subplots, applying the method described by Kirschbaum & Wirth (1995).

## Results

### Lichen diversity

A total of 42 lichen species was recorded along the 40 km transect (Table 1) with species diversity ranging between 12 and 22 species at the 25 sites. The average lichen species diversity for the sites closer to the coast (Sites 1–11) was 13.6 ± 0.4, which increased to an aver-

Table 1: List of observed and identified species. For the more common species relative frequency (%) as compared to the total frequency of all lichens (= 100%) at all sites are given in brackets

Taxon	%
<i>Acarospora ochrophaea</i>	
<i>Acarospora</i> sp.	
<i>Acarospora luederitzensis</i>	0.7
<i>Acarospora gypsi-deserti</i> ad int.	
<i>Buellia follmannii</i>	3.3
<i>Buellia incrustans</i>	6.1
<i>Buellia peregrina</i>	2.5
<i>Buellia sipmanii</i>	
<i>Buellia stellulata</i>	
<i>Caloplaca elegantissima</i>	2.2
<i>Caloplaca lactea</i> -group	
<i>Caloplaca namibensis</i>	7.0
<i>Caloplaca rubelliana</i>	
<i>Caloplaca</i> sp.	
<i>Caloplaca testudinea</i>	14.3
<i>Caloplaca volkii</i>	2.0
<i>Diploschistes henssenii</i>	
<i>Lecidea sarcogynoides</i>	
<i>Lecidella crystallina</i>	10.2
<i>Lecidella placodina</i>	
<i>Ramalina</i> cf. <i>angulosa</i> ("irritans")	3.3
<i>Ramalina</i> spec. II ("namibica")	
<i>Staurothele dendritica</i>	
<i>Teloschistes capensis</i>	5.1
<i>Toninia lutosalaustralis</i>	0.9
<i>Xanthoparmelia arrecta</i>	
<i>Xanthoparmelia hueana</i>	
<i>Xanthoparmelia dregeana</i> s.l.	12.7
<i>Xanthoparmelia equalis</i>	
<i>Xanthoparmelia evernica</i>	
<i>Xanthoparmelia follmannii</i>	
<i>Xanthoparmelia hottentotta</i>	
<i>Xanthoparmelia incomposita</i>	
<i>Xanthoparmelia lapidula</i>	
<i>Xanthoparmelia namibiensis</i>	
<i>Xanthoparmelia serusiauxii</i>	
<i>Xanthoparmelia tentaculina</i>	2.1
<i>Xanthoparmelia walteri</i>	11.1

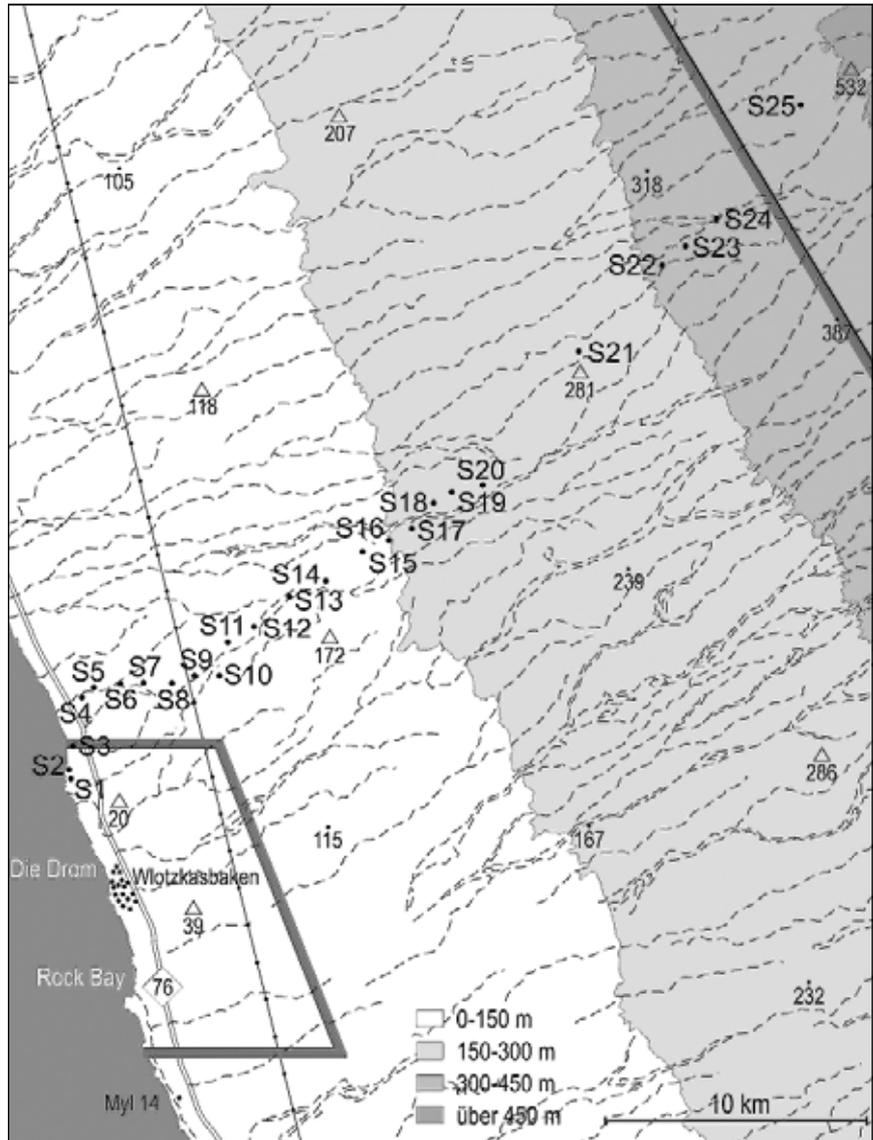


Fig. 1: Locations of the 25 investigated sites (Site 1 to Site 25) along the transect running from SW to NE. Broken lines = ephemeral creeks, thick lines = administrative units, unbroken thin line = power line, numbers triangles = altitude above sea level.

age of  $17.5 \pm 0.8$  on inland sites (Sites 12–25).

### Lichen cover and frequency

Near the coast, total lichen cover averaged 6% at Sites 1–3 with a cover as low as 3% recorded at Site 1 where the sparse lichen population displayed reduced vigour. A steep increase in lichen cover inland of Site 3 was observed, with 42.5% lichen cover recorded at Site 5, which was the highest value recorded along the entire transect (Fig. 2). This was mainly due to the presence of *Teloschistes capensis* (see also Fig. 3). A continuous decline in lichen cover was observed even further inland, to values of 9% at Site 22, 7.5% at

Site 23, 6% at Site 24 and 3% at Site 25, with one exception at site 17, which had 5% total lichen cover.

There was generally a poor correspondence between the cover of individual lichen species and their total frequency. A typical example was *Xanthoparmelia walteri* with a measured cover of less than 1%, but a recorded frequency of 100% at Site 14 (Figs. 2 & 3). Substantial heterogeneity in frequency of lichen species was observed between Site 1, where the average of the frequencies of all species was found at 6% and Site 8, where an average as high as 22% was recorded. However, total frequency of lichen species varied less between Site 14 and Site

24, where average frequencies ranged uniformly between 13.5% and 18.8%. Thus, frequency values do not reflect the decrease of lichen cover towards inland. The most common species in the study area was *Caloplaca testudinea* with a relative frequency of 15%, followed by species included in the *Xanthoparmelia dregeana* group (from the coast up to Site 10 almost exclusively *X. namibensis*, further inland mainly *X. dregeana* s.l. and *X. incomposita*), with relative frequencies ranging between 10.2% and 14.3%. Approximately one quarter of all observed lichen species displayed relative frequencies below 1%.

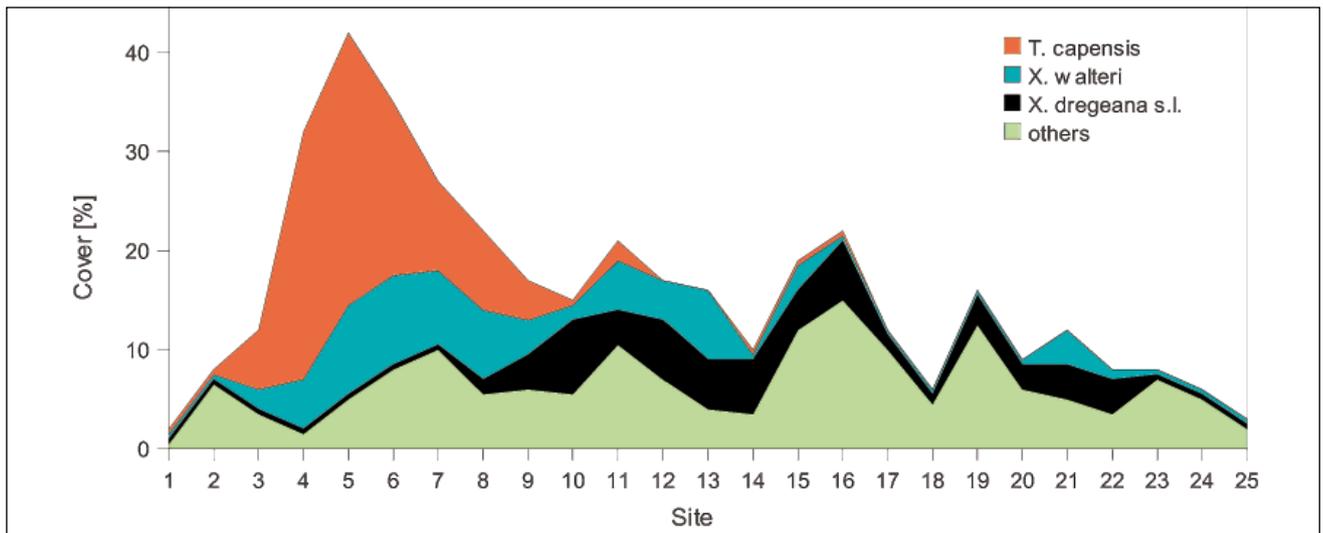


Fig. 2: Coverage (%) of *Teloschistes capensis*, *Xanthoparmelia walteri*, *Xanthoparmelia dregeana* s.l. and the coverage of all other observed species along the transect.

### Lichen distribution types

Four groups of lichen species with different distributions were distinguished. These were as follows:

**Distribution type 1 (*Caloplaca testudinea* group):** This group comprised eight lichen species present both inland and close to the coast. Eight species were distributed from the coast to the inland sites, of which *Buellia incrustans*, *Caloplaca testudinea*, *Lecidella crystallina*, brown species of the *Xanthoparmelia dregeana* group (without *X. tentaculina*), and *X. walteri* occurred throughout (Fig. 3). *Caloplaca namibensis* and *C. volkii* were absent at two sites, and *Toninia lutos/australis*, which generally occurred at very low frequencies, was absent from six sites.

Among the species belonging to the species complex of *Xanthoparmelia dregeana* s.l., *X. namibiensis* was distributed along almost the entire transect (recorded in Sites 1, 2, 4–10, 12, 16, 19, 21–24). Since this species could only be determined by thin layer chromatography of random samples next to plots, it is likely to have occurred at all sites along the transect.

Close to the coast, several species of this distribution type showed a relatively low frequency and often reduced vigour, such as *Caloplaca namibensis*, *Buellia incrustans*, *Xanthoparmelia walteri* and the *X. dregeana* s.l. (Fig. 3). Whereas *X. dregeana* s.l. and *X. walteri* attained

high frequency values between Sites 4 and 8 (i.e. the zone of the *Teloschistes* group, see below), the frequency of *Caloplaca volkii* and especially *C. namibensis* remained low in this area, and that of *C. testudinea* dropped considerably. Further inland of the *Teloschistes* zone, the frequency of *C. testudinea*, *C. namibensis* and *Xanthoparmelia dregeana* s.l. increased to up to 100%. Beyond Site 15 the frequencies of *Caloplaca namibensis* and *Xanthoparmelia walteri* decreased continuously, but transiently rose again at Site 21. Due to the discrepancy between the frequency of *Caloplaca namibensis* at the first ten sites and along the rest of the transect, this species showed a tendency to distribution type 3.

*Xanthoparmelia walteri* was present in nearly all quadrats from Sites 3 to 15, beyond which its frequency decreased and it occurred only occasionally at sites near the inland end of the transect. *X. dregeana* s.l., which reached a frequency of 100% at Site 8, maintained this frequency up to Site 22, despite a low cover value of only 1–4%.

**Distribution type 2 (*Teloschistes* group):** This group was composed of lichen species occurring from the coast up to Site 16, with their frequency or coverage decreasing from Site 12 at the latest. At least four species belonged to this group, i.e. *Xanthoparmelia tentaculina*, *Teloschistes capensis*, *Ramalina angulosa*, and *Xanthoparmelia hueana*. The

first two species occurred up to Site 16, the *Ramalina angulosa* complex (representing two species, whose proportions could not be differentiated, although both species were certainly present at Sites 4, 5 and 6) was only recorded up to Site 11 (Fig. 3), but otherwise behaved similarly to *Teloschistes capensis*. The vagrant lichen *Xanthoparmelia hueana* was confined to sites very close to the coast and the beginning of the *Teloschistes* field (Sites 1, 3, 4 and 5).

**Distribution type 3 (*Caloplaca rubelliana* group):** Species of this group were absent from the coastal section of the transect but occurred more or less far into inland areas. Approximately seven species belonged to this group. *Buellia peregrina* was present fairly regularly (14 times) from Sites 9 to 24 and *B. stellulata* (14 times) from Sites 7 to 25. *Acarospora luederitzensis* did not appear until Site 14, but then it occurred regularly; it was only recorded occasionally but was distributed equally in its range (Fig. 3). *Caloplaca rubelliana* (recorded 8 times: Sites 12, 14, 16–21), *Lecidella placodina* (recorded 10 times) and *Buellia follmannii* s.l. (recorded 12 times) first appeared at Site 12. Among the species of *Xanthoparmelia dregeana* s.l., *X. incomposita* (recorded 11 times: Sites 10 to 25) belonged to this group. *Staurothele dendritica*, although only present at Sites 18 and 20, may also be considered as a member of this distribution type.

**Distribution type 4 (*Xanthoparmelia serusiauxii* group):** The most characteristic members of this group were the two extremely drought-resistant foliose species *Xanthoparmelia evernica* (Site 23) and *X. serusiauxii* (Sites 24 and 25) with adnate thalli, and their appearance caused a distinct change in lichen vegetation. Other notable species that occurred furthest inland and even in extension to the transect were *Acarospora ochrophaea* (from Sites 19 to 25, with an isolated occurrence at Site 14; Fig. 3) and *X. lapidula* (Sites 21 and 25).

*X. dregeana* s.s. (Site 21), *X. equalis* (Site 25), *Acarospora "gypsi-deserti"* (Site 21, Sites 23–25, but also in Site 2 as a small thallus of reduced vigour) and a sterile grey areolated crustose species (cf. *Acarospora* sp.) (Sites 19 and 20) probably also belonged to this distribution type.

## Discussion

### Number of species

The number of more than 40 lichen species recorded along the transect is surprisingly high in view of the chosen sampling sites at very similar and uniform gravel plains. The increase in the number of species from coastal to inland sites was not expected considering the corresponding decrease in lichen cover and biomass (Schieferstein & Loris 1992). This change occurs rather abruptly from Site 11 inland, where fruticose lichens disappear. One reason for the relatively limited diversity in the *Teloschistes* zone is the rich development and high biomass of fruticose lichens, which outcompete crustaceous species growing close to the soil surface (see below). Further inland, in parallel with the disappearance of *Teloschistes*, biotic conditions are more favourable for crustose lichens. Another reason may be a greater diversity of suitable substrates, especially of dolerite pebbles, which are more conducive to the establishment of subneotrophic species.

### Lichen cover and frequency

Apart from the closely neighbouring sites (Sites 1 to 3), lichen cover is highest at the sites up to 4 km inland of the coast, a zone characterised by the dominance of *Telo-*

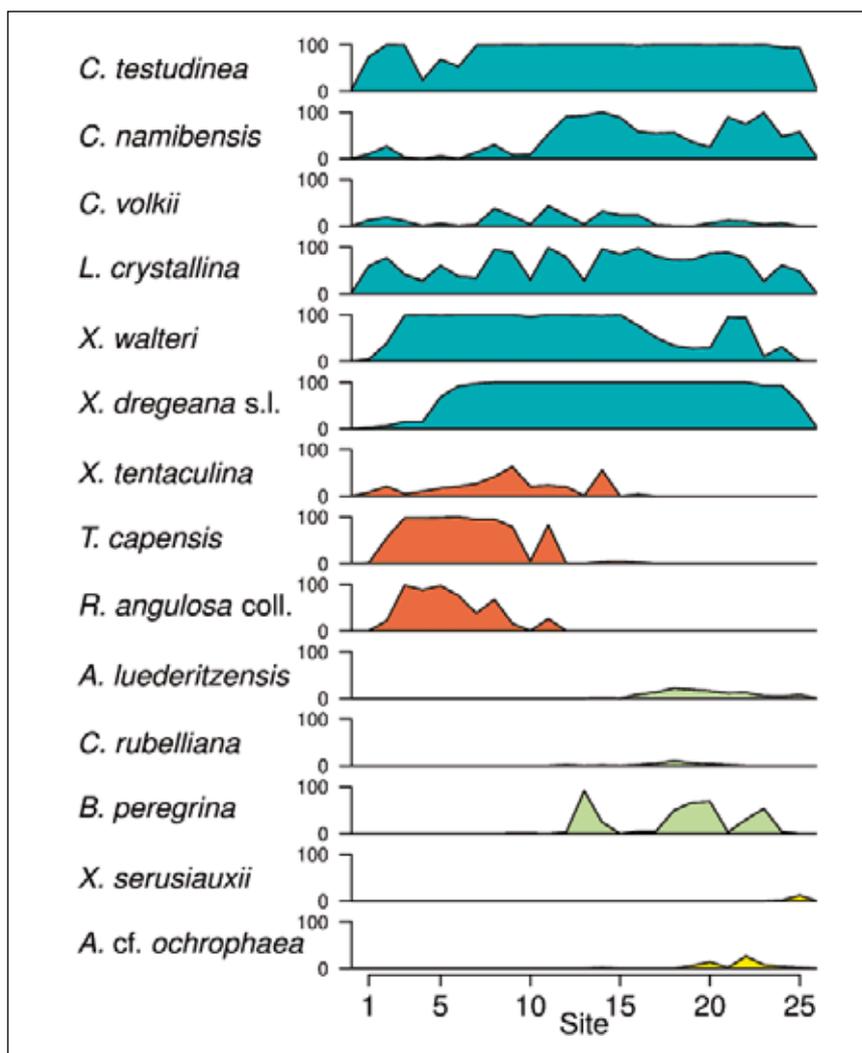


Fig. 3: Frequency (%) of selected lichen species along the transect. Distribution type 1: *Caloplaca testudinea*, *C. namibensis*, *C. volkii*, *Ledidella crystallina*, *Xanthoparmelia walteri*, *X. dregeana* s.l. Distribution type 2: *Xanthoparmelia tentaculina*, *Teloschistes capensis*, *Ramalina angulosa* coll. Distribution type 3: *Acarospora luederitzensis*, *Caloplaca rubelliana*, *Buellia peregrina*. Distribution type 4: *Xanthoparmelia serusiauxii*, *Acarospora ochrophaea*.

*schistes* and *Ramalina*. The high percentage cover of fruticose lichens is associated with poor cover of several crustaceous lichens, e.g. *Caloplaca testudinea* and *Buellia incrustans*. It can be assumed that the fruticose lichens intercept a high percentage of fog moisture, thus reducing the amount available for the crusts. Furthermore, *Teloschistes* cushions can be moved by wind, often with an attached crust of soil substrate. Where they accumulate they may cover pebbles and the crustaceous lichen species growing on them. Inland of Site 5, total lichen cover decreases significantly (Fig. 3), mainly due to the decline of *Teloschistes* itself (Fig. 2) and of *Ramalina* sp. The disappearance of *Teloschistes*, *Ramalina* and *Xanthoparmelia*

*tentaculina* is compensated for in terms of species numbers, but not cover, by the “inland-species” such as *X. incomposita* and *Caloplaca rubelliana*. Even the increase in cover of the crustaceous species of distribution type 1 (e.g. *Caloplaca testudinea*, *C. namibensis*, *Buellia incrustans*), which might be due to the absence of fruticose lichens, does not compensate for the loss of cover due to the disappearance of *Teloschistes* and *Ramalina*.

### Distribution of lichen species

Based on the distribution types 2, 3 and 4, it is possible to divide the Namib Desert into floristically defined sections (Wirth et al. 2007). In terms of distances, the first third to half of the transect up to Site 16

(about 15 km from the coastline) the lichen zone is characterised by the occurrence of *Teloschistes capensis*, *Ramalina* sp., *Xanthoparmelia tentaculina* and possibly *X. arrecta*. Inland from Site 16 the Namib is characterised by *Xanthoparmelia incomposita*, *X. lapidula*, *X. serusiauxii*, *X. evernica*, and the concentration of all *Acarospora* species. Functional types are unevenly distributed: fruticose species are confined to the coastal half of the transect and crustaceous lichens and *Xanthoparmelia* species with thalli reminiscent of placodioid crustose lichens dominate the inland half, and the only typical foliose lichen, *Xanthoparmelia walteri*, decreases considerably in cover and frequency here too.

Using a more detailed subdivision, four floristic-phytosociological sections can be distinguished. The first quarter (Site 1 to approximately Site 11) is delimited by a high percentage frequency of *Teloschistes*, the exclusive occurrence of *Ramalina angulosa* s.l. and *Xanthoparmelia hueana* and the constant presence of *X. tentaculina*; the second quarter (approximately Sites 11 to 16) is characterised by species, which are transient in nature with *Teloschistes* and *Xanthoparmelia tentaculina* quickly decreasing, *Caloplaca namibensis* (Fig. 3) and *Buellia peregrina* increasing, and *Xanthoparmelia incomposita*, *Caloplaca rubelliana*, *Lecidella placodina*, and *Buellia follmannii* s.l. appearing. In the third quarter (Sites 17 to 20) *Staurothele dendritica* is found, as well as species of *Acarospora*, namely *A. luederitzensis* (as from Site 14, Fig. 3) and *A. ochrophaea* (as from Site 19, Fig. 3). These species remain present in the last quarter (Site 21 to 25), which is characterised by the inland species *Xanthoparmelia serusiauxii*, *X. evernica*, *X. equalis*, *X. lapidula*, *Acarospora* “*gypsi-deserti*” and the optimal development of *A. ochrophaea*.

### Ecological conclusions

Reasons for the described distribution patterns of the lichen species along the transect are complex. Edaphic-petrographic factors probably do not play a decisive role (possibly with the exception of the calcicolous crust *Buellia peregrina*); they certainly have no influence

on the strikingly unequal distributions of species in the coastal areas (group 2, *Teloschistes capensis*, *Ramalina* sp., *Xanthoparmelia tentaculina*) or, for example, the decline of the important foliose lichen *Xanthoparmelia walteri*, since favoured substrates (quartz pebbles, gravel sand) are present throughout the length of the transect.

It is obvious, following the general assumption that fog precipitation decreases moving inland, that the high biomass and the luxurious development of lichens in the *Teloschistes* zone are clearly correlated with the particularly favourable moisture conditions close to the coast, and the decrease in cover and finally disappearance of the species of group 2 beyond Site 5 are related to successively more unfavourable conditions caused by diminishing moisture input.

Surprisingly, a significantly greater water input by fog precipitation close to the coast could not be confirmed by measurements in the lichen field of Wlotzkas Baken (close to Observatory S16). According to these measurements fog precipitation is a limiting factor further inland, but not along the coastal part of the transect and therefore does not significantly influence species distribution or biomass in the *Teloschistes* zone (Loris et al. 2004). Nevertheless, near the coast and in the first quarter of the transect, water relations for lichens are more favourable than further inland. The soaking of thalli after dew fall or fog moistening during the night lasts longer because the fog-bank disappears more slowly than further away from the coast—a well known phenomenon (Wirth, own observations). Furthermore, humidity often increases during the afternoon close to the coast with the consequence that fruticose lichens with their multibranched structure take up enough water vapour that the moisture compensation point may be reached (Lange et al. 1990). This probably occurs especially when stratus clouds migrate inland from the ocean, which happens quite often in the late afternoon. Investigations have shown that hydration remains above the compensation point for two hours longer in the zone of high biomass in comparison to inland sites (Loris & Pfiz,

unpubl.). This indicates a considerable surplus in carbon balance and is responsible for the high biomass at sites Sites 4 and 5. At least these data suggest there is an ecophysiological effective gradient in water supply from the coast to inland areas.

However, thunderstorms from the northeast and episodic warm winds, with or without transported sand, also play an important role (Loris et al. 2004, Loris et al. 2009) in lichen distribution. This is especially obvious with the vagrant lichen *Xanthoparmelia hueana*. This species, which does not shed attachment organs, is blown over the plots in the transect, but usually remains in sheltered depressions and between obstacles, as in the case of fruticose thalli in Sites 3 and 4. In a similar manner, wind or thunderstorms may have a considerable influence on the distribution of the easily transportable thalli of *Teloschistes capensis* and *Ramalina* sp. With strong winds these fruticose thalli together with interwoven *Xanthoparmelia walteri* are torn off, and whole tufts and cushions are lifted up with the adherent substrate, and blown away. The material is transported towards the coast, but gets partly trapped around obstacles such as plants (*Arthroa leubnitziae*, *Lycium tetradum*, *Galenia africana*, Mesembryanthemoideae) or protruding pebbles and rocks.

The restriction of *Xanthoparmelia tentaculina* to the *Teloschistes* zone cannot be explained by storm or leeward effects. A selective accumulation of small pebbles supporting this species by means of wind was not observed and must be excluded as an explanation. It is highly likely that the distribution of this species depends on the moisture gradient.

Similar investigations on mountain slopes almost 100 km further north support the argument that moisture gradients influence floristic changes. Wirth & Heklau (2006) found that only fog precipitation could be responsible for the considerable differences in species composition along transects, which also included a *Teloschistes* zone (at the wettest sites) and zones with *Caloplaca rubelliana* and *Xanthoparmelia serusiauxii* (at distinctly drier sites), where other “inland” species (group 3 and 4) were also found, e.g. *Acarospora*

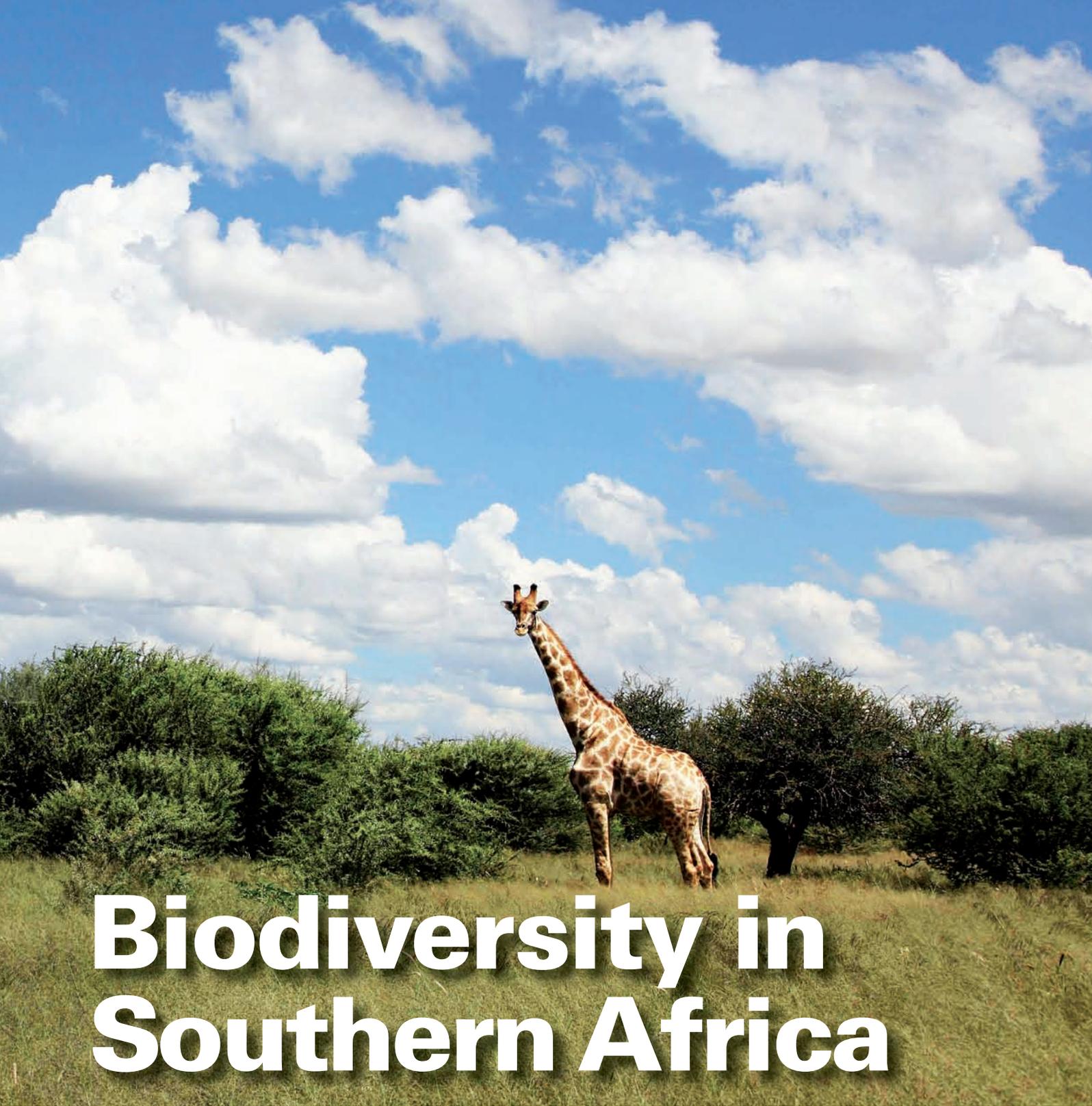
*luederitzensis*, *A. ochrophaea*, *Lecidella placodina*, *Xanthoparmelia incomposita*, and *Staurothele dendritica*. These species are apparently more tolerant to desiccation and better adapted to the relatively dry conditions towards the inland end of the transect. The dark colour of the dolerite substrate may also intensify the dry conditions of the sites by quickly warming the pebbles during insolation.

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Cover photograph: Giraffes on the game farm Omatako Ranch (Observatory S04 Toggekry) in the Namibian Thornbush Savanna.

Photo: Jürgen Deckert, Berlin/Germany.

Cover Design: Ria Henning

# Article III.3.7

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