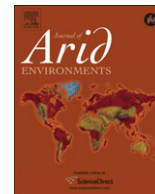


Contents lists available at [SciVerse ScienceDirect](http://www.sciencedirect.com)

Journal of Arid Environments

journal homepage: [www.elsevier.com/locate/jaridenv](http://www.elsevier.com/locate/jaridenv)

## Ecology and spatial patterns of large-scale vegetation units within the central Namib Desert

N. Juergens<sup>a,\*</sup>, J. Oldeland<sup>a</sup>, B. Hachfeld<sup>a</sup>, E. Erb<sup>b</sup>, C. Schultz<sup>c</sup>

<sup>a</sup> Biocentre Klein Flottbek and Botanical Garden, University of Hamburg (UHH), Ohnhorststraße 18, 22609 Hamburg, Germany

<sup>b</sup> Swakopmund, PO Box, 1224, Namibia

<sup>c</sup> European Space Agency (ESA), European Space Research and Technology Centre (ESTEC), Keplerlaan 1, P.O. Box 299, 2200 AG, Noordwijk, The Netherlands

### ARTICLE INFO

#### Article history:

Received 21 May 2012

Received in revised form

30 August 2012

Accepted 11 September 2012

Available online xxx

#### Keywords:

Classification

Database

Ecotone

Flora

Functional traits

Vegetation mapping

### ABSTRACT

This article offers a review of published knowledge and a new state-of-the-art analysis regarding the floristic composition, the functional composition and the plant communities found in the central Namib Desert. At the same time, this paper contributes to the understanding of the relationship between the plant species composition of the central Namib Desert and the prevailing environmental gradients, with an emphasis on diversity and ecology in space and time. This article builds on three thematic foci. The first focus (1) lies on the present knowledge of the composition and the characteristics of the flora. A comprehensive floristic database has been compiled based on all available sources. A second focus (2) lies on the characterization and spatial distribution of the vegetation units. Therefore, we created a new vegetation classification based on a unique vegetation-plot database (<http://www.givd.info/ID/AF-00-007>) and additional data summing up to 2000 relevés, resulting in 21 large-scale vegetation classes. Using a supervised classification approach based on the vegetation classification, remote sensing and environmental data, we were able to produce a new vegetation map of the Central Namib. This was updated using expert knowledge, field visits and through manual preprocessing. With the third focus (3) we explore the spatial patterns of the previous foci and discuss their relation to environmental parameters and gradients.

© 2012 Elsevier Ltd. All rights reserved.

### 1. Introduction and study area

Vegetation is generally sparse in the Namib Desert, which forms a narrow strip along the west coast of southern Africa (Jürgens, 1991; Werger, 1978). However, in the Namib adaptation of plants to aridity commenced long before the formation of modern ocean currents (Ward et al., 1983). This long history of aridity led to the evolution of several very specific pools of endemic plant species, which are spatially distributed according to their environmental needs. However, until today, a spatially explicit approach to the different vegetation units of the Namib that would allow for a more in-depth analysis of this very old desert is still missing.

The present lack of a vegetation map is accompanied by the lack of a systematically sampled body of adequate data and a robust

classification based on objective methods. Therefore, no environmental understanding of vegetation units could evolve, and hence no conceptual framework for conservation purposes and for more specific ecological research could be developed. The here presented study aims at filling these important gaps. We studied the combination of plant species within vegetation units in the study area and its spatial subunits. In this paper, special attention is given to the correlation between environmental gradients in space (and to a lesser extent in time) and the related pools of plant species defined by their structural and physiological adaptations. This format also allows for a review of published studies with regard to earlier vegetation mapping efforts.

The study area covers the Central Namib between and including the Ugab and Kuiseb catchments as its latitudinal boundaries, while it is bounded by the Atlantic Ocean in the west and the escarpment in the east. The Brandberg forms a very specific azonal element and is not part of this study.

Earlier definitions of the Central Namib follow a similar concept (e.g. Giess, 1971). A minor difference is that we do not use the Ugab or Huab rivers as the northern boundary but include those parts of the Ugab catchment located north of the study area.

\* Corresponding author. Tel.: +49 4042816260/+49 1701666500 (mobile); fax: +49 4042816261.

E-mail addresses: [norbert.juergens@t-online.de](mailto:norbert.juergens@t-online.de), [juergens@botanik.uni-hamburg.de](mailto:juergens@botanik.uni-hamburg.de) (N. Juergens), [oldeland@botanik.uni-hamburg.de](mailto:oldeland@botanik.uni-hamburg.de) (J. Oldeland), [berit\\_hachfeld@yahoo.com](mailto:berit_hachfeld@yahoo.com) (B. Hachfeld), [erbelke@mweb.com.na](mailto:erbelke@mweb.com.na) (E. Erb), [christoph@familie-schultz.de](mailto:christoph@familie-schultz.de) (C. Schultz).

The same approach is applied to the Kuiseb, in spite of the fact that to the South of the Kuiseb, no really productive catchment can be identified within the dune field. We decided to take the southern boundary of the Erongo Region as the southern limit, with a line running from just south of Sandwich Harbour to the Koichab Pan.

Strictly speaking, lichens are not regarded as plants and lichen fields are not regarded as vegetation units. On the other hand, vast areas of the coastal Namib are nearly devoid of higher plants but show an extraordinary cover and a very high species richness of lichens (Loris and Schieferstein, 1992; Schieferstein, 1989; Walter, 1936). Because of their exceptional importance, the lichen fields are therefore included in this article.

## 2. Material and methods

This study is based on comprehensive databases of the flora, the vegetation and environmental parameters of the Central Namib. Lichen fields are also included because of their importance within the fog belt of the coastal Namib.

### 2.1. Floristic database

All available knowledge regarding the observation of plant taxa within the study area has been compiled and processed with a consistent nomenclature following the Windhoek Herbarium using BiotaBase (Muche et al., 2012) and BIOTACollections (Muche and Jürgens, 2011) as database software. This floristic database encompasses (a) all herbarium records of the study area recorded at the herbaria of Windhoek (WIND), Pretoria (PRE) and Hamburg (HBG), (b) published point occurrence data from relevant projects, e.g. the Namibian Tree Atlas Project (Curtis and Mannheimer, 2005) and numerous taxonomic and floristic articles, as well as (c) own field data. The resulting floristic database contains more than 65,000 records of plant point data from the study area.

The compilation of all species records from the herbaria (WIND, PRE, HBG), the literature and the vegetation-plot database (see below) first resulted in a total of 1085 species. Each of these species was checked for (a) correct taxonomic status (excluding 59 names), (b) superfluous names following the hierarchy of species, subspecies and varieties (excluding another 68 names) and (c) a robust confirmation of occurrence in the study area (excluding 107 names). It was not possible to verify all specimens in the respective herbaria so that the entire species pool could not be identified to our complete satisfaction. Another 44 species are therefore still regarded as uncertain since it was impossible to see all specimens in the herbaria because of insufficient evidence (e.g. one single record in a list within one publication only or because no reference to specimen has been made).

### 2.2. Vegetation-plot database

A vegetation-plot database using the same consistent taxonomic nomenclature has been generated using BiotaBase (registered at [www.GIVD.info](http://www.GIVD.info) under ID: AF-00-007; Dengler et al., 2011). Data compiled since the early 1990s formed the basis for classifying species assemblage data into major vegetation types. For the classification, 2000 relevé data sets (B. Hachfeld: 949, N. Juergens: 897, B. Strohbach: 154), using a standard size of 1000 m<sup>2</sup>, including geographic coordinates, habitat information and all observed species occurrences with percentage cover estimates and (partly) abundance data were used. We evenly sampled the spatial diversity of the Central Namib by taking records at regular intervals and in all distinguishable vegetation and habitat types. The geographical spread of samples was homogeneous with two exceptions: First,

the dune field south of the Kuiseb River could not be sampled but in a few places. Second, the density of relevés is slightly lower at the eastern margin of the study area.

It is worth mentioning that both plant databases have been extended over many years, thereby including different seasons as well as dry and wet years. Many relevés do not show the entire local species pool at the time of documentation. This must be taken into consideration when interpreting occurrences of therophytes, geophytes and hemicryptophytes. Conditions of strongly grazed plant individuals in particular during dry seasons may have resulted in some inconsistencies in plant identifications, e.g. *Stipagrostis hirtigluma* ssp. *hirtigluma* versus *Stipagrostis uniplumis* var. *intermedia*.

### 2.3. Lichen database

As strong relationships exist between the form (morphology) of crust organisms and their ecological function (Rogers, 1977), the concept of morphological groups was used to locate 874 homogeneous reference sites (Eldridge and Rosentreter, 1999). At these sites, spectral properties of lichens were collected *in situ* using an ASD FieldSpec FR spectroradiometer covering the 350–2500 nm spectral range at a spectral resolution of 1 nm. Using this reference data set, a hierarchical classification scheme for mapping the distribution of lichen fields in the central Namib Desert based on remote sensing data was created (Schultz, 2006).

### 2.4. Environmental parameters

Environmental gradients were integrated into the vegetation mapping strategy. The data set consists of the following data: (1) climatic data were extracted from the 30 arc-seconds resolution WorldClim data set (Hijmans et al., 2005), which represents globally averaged climate data for the period 1950–2000; (2) a digital elevation model (DEM) was generated on basis of the 1 arc-second resolution ASTER-GDEM version 1.0 elevation data set (METI/NASA, 2009). Based on the DEM covering the whole Central Namib with a 30 m grid resolution, several ecologically relevant topographical parameters were derived, among others (3) inclination in degree, (4) exposition, (5) diurnal anisotropic heating, which represents a continuous measure of exposition dependent energy (Hengl and Reuter, 2011), and (6) the vector ruggedness measure (VRM, Sappington et al., 2007), which measures landscape roughness. A digital geological map (7) at a scale of 1:250,000 was provided by the Geological Survey of the Ministry of Mines and Energy (MME) of Namibia. Furthermore, median, minimum, maximum and range of satellite derived measures of biomass were calculated from a monthly data set of 2010 global MOD13Q1 EVI (EVI = Enhanced Vegetation Index) images with a ground resolution of 250 m (NASA LP-DAAC, 2010). Furthermore, two fully pre-processed Landsat 7 ETM + scenes (Path/Row/Date: 180/75/2003-04-22; 179/76/2003-05-01) were utilized for the mapping and supervised classification of the distribution of the lichen-dominated biological soil crust communities. Based on Landsat 7 ETM + acquisitions, satellite mosaic data (RGB channels = 7–4–2) were used for the vegetation mapping task for the entire study area (MDA, 2004). See Table 1 for a list of all assembled data sets.

### 2.5. Vegetation classification

For vegetation classification, an initial set of 1574 relevés with 440 species and their cover values were extracted from AF-00-007 and imported into the phytosociological classification software JUICE 7.0 (Tichý, 2002). Within JUICE, a numerical pre-classification was carried out using hierarchical clustering of relevés by square

**Table 1**  
Overview on the environmental raster data used for spatial modeling.

ID	Parameter	Short	Derived from	Literature
1	Isothermality [°C]	Bio3	WORLDCLIM	Hijmans et al. (2005)
2	Maximum temperature of warmest month [°C]	Bio5	WORLDCLIM	Hijmans et al. (2005)
3	Mean temperature of wettest quarter [°C]	Bio8	WORLDCLIM	Hijmans et al. (2005)
4	Mean annual sum of precipitation [mm]	Bio12	WORLDCLIM	Hijmans et al. (2005)
5	Vector ruggedness measure [unitless]	vrm	DEM	Sappington et al. (2007)
6	Diurnal anisotropic heating [Energy/cell]	Dah	DEM	AG Boden (1994)
7	Geological units [71 classes]	Geol	MME Namibia	Citation not available
8	MODIS-EVI median [EVI]	EVImed	MODIS TS	Hengl and Reuter (2011)
9	MODIS-EVI range [EVI]	EVIran	MODIS TS	Hengl and Reuter (2011)
10	MODIS-EVI min [EVI]	EVImin	MODIS TS	Hengl and Reuter (2011)
11	MODIS-EVI max [EVI]	EVImax	MODIS TS	Hengl and Reuter (2011)
12	Landsat mosaic S-33-2000 [RGB 7–4–2]	Geocover	ETM Mosaic	MDA (2004)

The bioclimatic variables derived from the WorldClim data set represent mean annual trends from the past 50 years. The abbreviation EVI refers to Enhanced Vegetation Index, a vegetation index derived from MODIS satellite data. The Landsat Mosaic was available as RGB image, where the spectral channels of the satellite were arranged in the order of channel 7, 4 and 2.

root-transformed species abundances. The applied distance measure was Bray–Curtis distance, and the linkage algorithm was ‘Flexible beta’ with beta set to  $-0.25$ . We used the internal algorithm ‘OptimClass’ (Tichý et al., 2010) of JUICE to find an optimal number of clusters based on the highest number of diagnostic species. This initial vegetation classification resulted in about 53 small vegetation units, which were then iteratively further aggregated based on expert knowledge and investigation of the synoptic tables. Reordering, shifting and merging of small into large clusters led to large vegetation units that (a) comprise a set of diagnostic species (species with a high fidelity within a certain cluster) and (b) are spatially recognizable, i.e. relevés are not randomly scattered, but show a certain spatial pattern. Finally, a satisfactory classification of 21 vegetation types was achieved.

### 2.6. Production of a new vegetation map

The vegetation mapping covered three major steps: (i) identification of major vegetation units based on a vegetation-plot database (see Section 2.5), (ii) supervised classification of environmental data sets (Table 1) with vegetation plots coded as vegetation types and (iii) post-processing of spatial extents of vegetation units based on expert knowledge.

Various possibilities exist for the spatial extrapolation of vegetation plot-based information. In the present study, we used a standard maximum likelihood-based supervised image classifier. Besides satellite imagery (MODIS, Landsat ETM 7), climatic data and topographic data were used as auxiliary information for the classification (Table 1). A total of 70% of vegetation plots from each vegetation unit were used as training areas for the classifier while 30% of each vegetation unit served as a validation data set. In order to increase the area available for the supervised classifier, a rectangular buffer of 500 m was placed around each vegetation plot. All processing of raster data was carried out in GRASS-GIS (Neteler and Mitasova, 2008), while supervised modeling was done with SAGA-

GIS (Böhner et al., 2006). As a measure of map accuracy, we calculated Cohen's Kappa (Horning et al., 2010) based on predicted and observed vegetation units. The resulting Kappa value was 0.45 and thus only moderately high.

On the classified raster map we identified several errors, such as areas that were either too small or too large or vegetation units that definitely could not exist at a location predicted by the model, e.g. in some areas the beach vegetation unit was predicted too far inland. The raster map was therefore converted into a polygon map for final post-processing based on expert knowledge. From August to December 2010, N. Jürgens verified the spatial extent of vegetation types with uncertain boundaries on several excursions.

About 350 newly sampled relevés were integrated into the vegetation classification. The new relevés sharpened concepts and new boundaries of vegetation units. Post-processing comprised manual editing of vegetation type boundaries based on the inclusion of vegetation borders visible in Google Earth imagery (Google Inc., 2011), e.g. for the western boundary of the transition to savanna. These editions were integrated into the vegetation map. All further manual editions were cross-checked with the AF-00-007 and by expert knowledge (N. Jürgens).

### 2.7. Lichen field mapping

Following the establishment of a hierarchical classification scheme using homogenous reference sites and analyses of spectral signatures collected *in situ*, a fuzzy likelihood classification was performed on a stratified data set. While classification techniques utilizing “hard classifiers” assign each pixel to only one class, with fuzzy classification techniques, often referred to as “soft classifiers”, only a membership grade is assigned to the classified pixel (Zhang and Kirby, 1999). For this study, the assignment of pixels to classes is described by the Mahalanobis distances in a fuzzy way as no input/output information is given but information describing a “more or less” membership. Rule-based defuzzification based on the membership values was realized using a kernel-based convolution filtering. Classification accuracy for the northern part of the study area (180/75) was a calculated Cohen's Kappa of 0.82, whereas the southern part of the study area showed a Cohen's Kappa of 0.80. The lichen field classes were merged later with the vegetation map described in Section 2.6.

## 3. Results and discussion

### 3.1. Flora

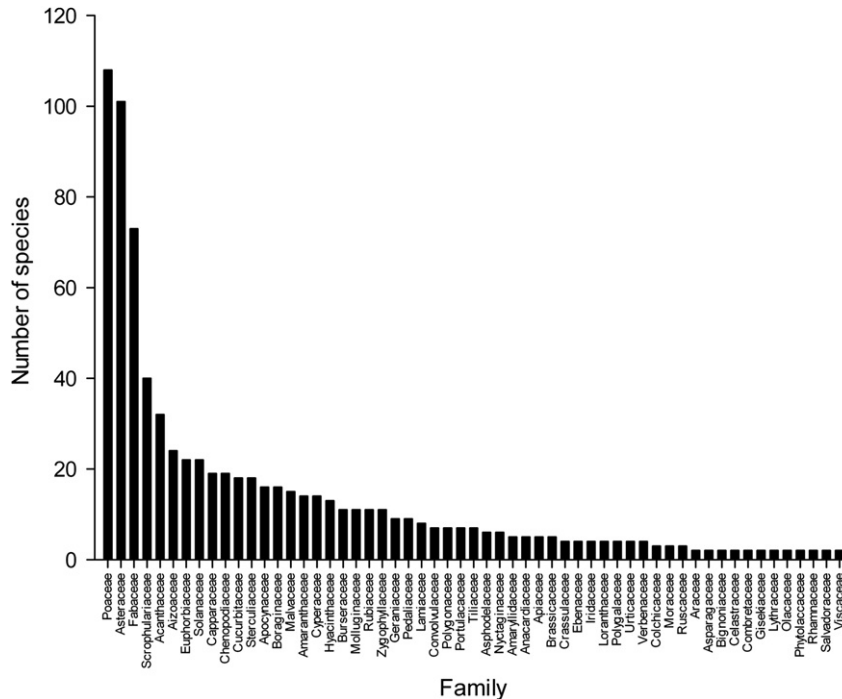
Within the central Namib Desert (as described above and excluding the Brandberg), 806 seed plant species (spermatophytes) (Appendix 1) were confirmed by the floristic database.

#### 3.1.1. Phylogenetic subdivision

The 806 seed plants belong to 93 plant families, with Poaceae (108 species), Asteraceae (101), Fabaceae (73), Scrophulariaceae (40 species), Acanthaceae (32 species), Aizoaceae (24 species), Euphorbiaceae (22 species) and Solanaceae (22 species) representing the dominant number of species (Fig. 1).

#### 3.1.2. Endemicity

Of these 806 Central Namib species, 103 species (=12.8%) are endemic to Namibia, with an additional 27 near-endemics (additional 3.3%). Sixteen species (2.0%) are regarded as endemics or near-endemics for the study area. This comparatively low proportion of endemics is caused by the broad latitudinal extension of most species' distribution areas, which run essentially parallel to

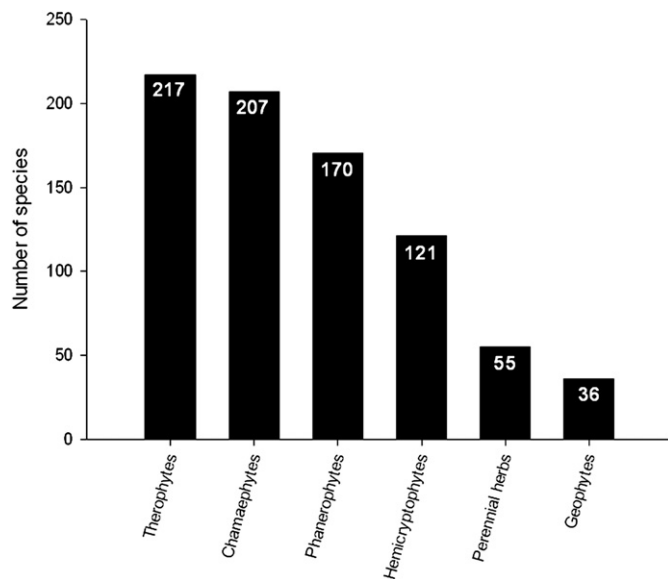


**Fig. 1.** Plant families found in the study area ranked by their species richness. Families with only one species (not shown): 58, Aponogetonaceae; 59, Campanulaceae; 60, Caryophyllaceae; 61, Commelinaceae; 62, Elatinaceae; 63, Frankeniaceae; 64, Hydnoraceae; 65, Illecebraceae; 66, Juncaceae; 67, Loasaceae, 68, Montiniaceae; 69, Moringaceae; 70, Myrothamnaceae; 71, Neuradaceae; 72, Oleaceae; 73, Ophioglossaceae; 74, Orobanchaceae; 75, Oxalidaceae; 76, Papaveraceae; 77, Passifloraceae; 78, Plumbaginaceae; 79, Potamogetonaceae; 80, Ranunculaceae; 81, Resedaceae; 82, Ruppiaceae; 83, Rutaceae; 84, Santalaceae; 85, Sapindaceae; 86, Tamaricaceae; 87, Tecophilaeaceae; 88, Typhaceae; 89, Vahliaaceae; 90, Velloziaceae; 91, Vitaceae; 92, Welwitschiaceae; 93, Zannichelliaceae.

the coastline. As a consequence, the majority of taxa also occur either north or south of the study area.

### 3.1.3. Life forms

The life-form spectra include 377 woody species (207 dwarf shrubs, 170 shrubs and trees) and 429 species adapted to the arid environment by periodic or facultative shoot reduction during annual dry seasons or years of extended drought (121 hemicyptophytes, 36 geophytes, 55 perennial herbs, 217 therophytes) (Fig. 2, Appendix 1).



**Fig. 2.** Number of species found for each life form in decreasing order.

### 3.1.4. Succulence

Eighty-five plant species store water in above-ground organs (78 succulents, seven weakly succulent). Of these, 45 are leaf-succulent species (plus nine with only weakly developed leaf water storage), 41 species store water within their stems, and nine species combine both strategies (for details see Appendix 1). The highest density of leaf-succulent species is found within the temperate vegetation units (5–10, see Section 3.4.2), close to the cooling and moisture-providing Benguela upwelling system.

Of the 41 stem-succulent species, 17 have developed a bark, leaving primary production to leaves generated only during the wet season. Twenty-four of the stem succulents retain a green photosynthetically active primary cortex throughout their life time (“green stem succulents”) and are thus able to maintain primary production during the leafless season. Of these, 18 species show a rod-like stem morphology with a typical diameter between 5 and 20 mm. In contrast, six of the stem succulents that are not covered with bark are cactoid, with prominent ridges or tubercles facilitating the expansion and shrinking of the stem during dry and wet phases (for details see Appendix 1).

### 3.1.5. Longevity

A hitherto underrated peculiarity of the flora of the Namib Desert is the longevity of the individuals of many species. The very high life span is closely related to the species’ ability to make use of rare events to sustain populations. Two examples demonstrate this:

**Example 1.** Within the coastal zones, the landscape is characterized by shrubs of *Arthroa leubnitziae*, which is the dominant species in most of these areas. Interestingly enough, no rejuvenation could be described in any natural habitat of this species for the past decades, with the exception of individuals next to scraped roads, railway lines and other disturbed sites. Germination and establishment in the wider surroundings of the town of

Swakopmund was restricted to a very few single individuals in natural habitats, in spite of several large rainfall events occurring during the last four decades (own observation E. Erb). There is evidence from repeat photography as presented in the comparison in Fig. 3 (1917–2005) that even in 1934, the rainiest year on record, no noteworthy establishment of new individuals of *A. leubnitziae* took place. Until today it is unknown what type of rainfall event may have triggered the germination and establishment of the plants characterizing the vegetation today. It is also unknown when such an event may have taken place.

**Example 2.** Populations of *Welwitschia mirabilis* also show an extremely slow turnover if not located within a river bed (Fig. 4). Again, over a period of 120 years, no important change took place (Jürgens, 2006).

There have been exceptional rain years during the past decades. The immediate effects of one such rain year has been documented (Hachfeld, 2000). However, also this event triggered neither the germination nor the establishment of *A. leubnitziae* or *W. mirabilis*. This knowledge gap underlines the need for long-term observation studies including the level of communities, populations and individuals.

### 3.2. Vegetation classification and mapping – background

A detailed vegetation survey for this region does not exist (Strohbach and Jürgens, 2010). Until today, attempts to classify and map the plant cover of the Central Namib either aimed at a much

larger scale or covered only a small area within the Central Namib. A consistent classification or map of the Central Namib is still missing.

At large scales there are the following works: (a) a broader habitat classification into 'Inner Namib', 'Pro-Namib', etc. (Jürgens et al., 1997; Walter, 1936), (b) a phytogeographical subdivision (Jürgens, 1991, 1994; Robinson, 1975; Werger, 1978), (c) the large vegetation map of whole Namibia (Giess, 1971, 1998) or (d) of whole Africa (White, 1983). The largest spatial scale was used by Robinson (1976), who covered the southernmost part of the Central Namib from roughly 23°S (latitude of Walvis Bay) to the Kuiseb River vicinity. Robinson sampled 472 relevés of mostly 50 m<sup>2</sup> (5 m × 10 m) and classified them into six community groups with numerous sub-communities. Due to the lack of an exact spatial reference system he was not able to generate a seamless vegetation map but single distribution maps for 23 communities. Because of the small relevé size and the lack of data on the exact localities we did not integrate his relevés into our map. Nevertheless, the boundaries of the communities proposed by Robinson match well with our findings.

Small-scale vegetation has either been classified (Burke et al., 2008; Cowlshaw and Davies, 1997; Hachfeld and Jürgens, 2000; Hachfeld, 1996; Jürgens et al., 2010) or mapped (Burke, 2008) or classified and mapped (Robinson, 1976) or mapped on basis of a remote sensing classification with validation steps (Schultz, 2006), mostly in smaller areas or for specific components such as lichen fields.

Extensive spatial analyses of the distribution of central Namib Desert lichen communities have been presented by Wessels and



**Fig. 3.** Repeat photography of the landscape southeast of the Roessing Mountain illustrating the extremely slow vegetation dynamics in the Central Namib. The upper photo was taken in November 1917 by Carl Schulte (Accession nr. PA 15-54 a/b at the Sam Cohen Library, Swakopmund). There are numerous individuals of predominantly two plant species, mainly arranged as linear patterns along drainage lines. The compact dark dwarf shrubs are *Arthroerua leubnitziae* (Amaranthaceae), while the larger shrubs with a twiggy periphery are *A. reficiens* (Fabaceae). Both species exploit soil water, but only *Arthroerua* is able to make use of fog water combed out of the frequent coastal fog. The lower picture was taken in 2005 by N. Juergens and E. Erb. The comparison shows that almost all plant individuals alive in 2005 already existed in 1917, almost 90 years earlier.



Fig. 4. Repeat photography of Welwitschiavlake taken in 1884 (top: Schenck, 1903) and in 2004 (bottom: N. Juergens and E. Erb) at the same location.

van Vuuren (1986), Schieferstein (1989), Loris and Schieferstein (1992) and Schultz (2006). Following the definition by Schieferstein (1989) and Loris and Schieferstein (1992), a lichen field is an extended plain area of at least 4 km<sup>2</sup> that is densely covered by lichens. This definition was substantiated by Jürgens and Niebel-Lohmann (1995) with the addition that lichen fields are “plant formations of considerable surface area, in which epilithic (saxicolous) to epipsammic (terricolous) lichens play the dominant role with respect to structure, cover and biomass, if compared with ferns and seed plants”.

### 3.3. A new vegetation classification

The classification of the vegetation based on the 1547 relevés stored in the vegetation plot database resulted in 53 small vegetation units based on the floristic composition, which were regrouped into 21 large-scale vegetation units (see Section 2.5). Three additional units were defined separately, namely Brandberg mountain vegetation, Walvis Bay urban area and Sandwich Harbour. Within unit 7 there are five subunits covering the different types of lichen fields (Table 2).

The distribution areas of the plant species subdivide the entire Namib into different regions. These phytogeographical patterns are controlled by environmental factors as well as by the history of evolution and ecology. The resulting spatial patterns offer valuable information on the relative importance of different environmental parameters for plants. A vegetation hierarchy based on the mean dissimilarity of diagnostic species abundances per vegetation unit is presented in Fig. 5. This hierarchy will also be used to introduce and discuss the single vegetation units in Section 3.4. This hierarchy of dissimilarities with respect to the composition of plant species and their ecological correlates deserves special attention because it

allows a botanical point of view on the environmental diversity of the central Namib Desert.

#### 3.3.1. First hierarchical division

As a first division, (1) the vegetation of the coastal units (including mobile dunes and riparian vegetation of the large rivers) is separated from (2) the vegetation of all grasslands, shrublands and the transition to savanna located further inland.

This division is interpreted as part of the large-scale differentiation into the (1) Greater Cape Flora with the Succulent Karoo elements, related to temperate winter rainfall or high air humidity climate within the first 40–50 km from the coast into the (2) palaeotropical vegetation, related to the tropical summer rainfall climate of either the Nama Karoo or the Sudano-Zambeian Savanna biome.

#### 3.3.2. Second hierarchical division within the temperate unit

At the second hierarchical level, the first group splits up into (1.1) the mobile dunes (unit 1) and (1.2) all other units within the temperate climate.

Ecologically, we conclude that at this level the substrate defines environmental conditions rather than the climatic differences within the temperate zone.

#### 3.3.3. Third hierarchical division within the temperate unit

After exclusion of the mobile dune fields, the vegetation of the large dry river beds (unit 3) and salt marshes (unit 4) are separated from all remaining temperate habitats.

#### 3.3.4. Fourth hierarchical division within the temperate unit

The coast-inland zonation is only reflected at this level: The vegetation units 5 (*Salsola nollothensis*–*A. leubnitziae* coastal desert plain shrubland), 6 (*Zygophyllum clavatum*–*Brownanthus kuntzei* coastal dwarf shrubland), 7 (*A. leubnitziae*-dominated fog belt units, including the lichen fields), 8 (*A. leubnitziae*–*Zygophyllum stapffii* succulent shrublands) and 10 (*A. leubnitziae*–*Z. stapffii* – grassland transition) form a narrow belt running parallel to the coast, following each other in the listed sequence. Only unit 9 (Coastal rocky desert dolerite hills) forms an azonal unit. Dolerite ridges with large basalt boulders create a range of peculiar habitat types, which support a similar species composition wherever such dolerite ridges occur within the zonal units 7, 8 and 10.

#### 3.3.5. Second, third and fourth hierarchical division within the tropical unit

It is of similar interest to follow the cluster hierarchy with regard to the tropical units. These divisions separate all grasslands from the Nama Karoo shrublands and the transitions to proper savanna.

The various grasslands are separated based on their dominant grass species, partly reflecting preference for more sandy soils (*Stipagrostis hochstetteriana* (19, 20) and *Stipagrostis ciliata* (11)), calcrete soils (*Stipagrostis obtusa* (12, partly also on sandy soils) and further east *Eragrostis nindensis* (13)), gypsum and clay soils (*Stipagrostis gonatostachys*, *Stipagrostis subacaulis* (11)) and more rocky soils (*S. hirtigluma*, partly *S. uniplumis* in vegetation units 14, 16 and 17).

Only those woody vegetation units that occur on shallow soils and that characterize the transition to the different savanna units (*Acacia reficiens* savanna, *Colophospermum mopane* savanna) represent zonal vegetation units. The shrubby and partly stem-succulent (e.g. *Commiphora* spp., *Euphorbia damarana*) units (15) and (18) rather reflect the more rocky habitat types. They stretch parallel to the major erosion structures along the Khan, Omaruru, Swakop, Kuiseb and Cape Cross river systems (see Section 3.4).

In summary, both climate (partly driven by topography) and substrate control the spatial pattern of vegetation units, as in many

**Table 2**

Characterization of identified vegetation units. Given are the ID (compare Fig. 5), the corresponding biome, the name of the vegetation unit and its area in hectare and percent.

Nr.	Phytogeography	Vegetation unit	Area [ha]	Area [%]	n	Spp.
1	Azonal	<i>Stipagrostis sabulicola</i> – <i>Cladoraphis spinosus</i> mobile dune grasslands	243,645	5.90	29	2.3
2	Azonal	<i>Faidherbia albida</i> – <i>Acacia erioloba</i> large ephemeral river riparian woodlands	15,281	0.37	86	7.3
3	Azonal	<i>A. reficiens</i> – <i>Boscia foetida</i> small ephemeral river riparian woodlands	0	0.00	95	20.5
4	Azonal	<i>Odysea paucinervis</i> salt marsh	8284	0.20	10	3.5
24	Azonal	Sandwich Harbour Lagoon	5421	0.13	0	0
25	Azonal	Walvis Bay (urban area and Pelican Point)	11,569	0.28	0	0
	Azonal units		284,200	6.88		
5	Succulent Karoo	<i>Salsola nollothesis</i> – <i>Arthroa leubnitziae</i> coastal desert plain shrublands	68,452	1.66	22	4.6
6	Succulent Karoo	<i>Zygophyllum clavatum</i> – <i>Brownanthus kuntzei</i> beach succulent dwarf shrublands	16,963	0.41	24	3
7	Succulent Karoo	<i>Arthroa leubnitziae</i> -dominated fog belt shrublands	502,098	12.15	156	3.7
7	Succulent Karoo	<i>Arthroa leubnitziae</i> fog belt shrubland with fruticose–foliose lichen zones	7578	0.18	n.a.	n.a.
7	Succulent Karoo	<i>A. leubnitziae</i> fog belt shrubland with foliose crustose lichen zones	12,730	0.31	n.a.	n.a.
7	Succulent Karoo	<i>Arthroa leubnitziae</i> fog belt shrubland with fruticose–foliose–crustose lichen zones	54,404	1.32	n.a.	n.a.
7	Succulent Karoo	<i>Arthroa leubnitziae</i> fog belt shrubland with fruticose–crustose lichen zones	982	0.02	n.a.	n.a.
7	Succulent Karoo	<i>Arthroa leubnitziae</i> fog belt shrubland with crustose lichen zones	18,503	0.45	n.a.	n.a.
8	Succulent Karoo	<i>Arthroa leubnitziae</i> – <i>Zygophyllum stapffii</i> coastal plains succulent shrublands	329,807	7.98	233	6
9	Succulent Karoo/ Azonal	<i>E. giessii</i> – <i>P. otaviense</i> coastal dolerite hills succulent shrublands	1530	0.04	79	9.4
10	Succulent Karoo/ Nama Karoo Coastal zones	<i>Arthroa leubnitziae</i> – <i>Zygophyllum stapffii</i> – <i>Stipagrostis ciliata</i> desert plains transitional succulent shrub- and grasslands	446,426	10.80	124	11.9
			1,459,472	35.32		
11	Nama Karoo	Species-poor <i>Stipagrostis ciliata</i> – <i>Stipagrostis gonatostachys</i> central desert plains grasslands	181,649	4.40	166	5.9
13	Nama Karoo	<i>Stipagrostis obtusa</i> central calcrete desert plains grasslands	437,240	10.58	73	6.8
14	Nama Karoo	<i>Eragrostis nindensis</i> eastern calcrete plains grasslands	522,239	12.64	114	12.8
15	Nama Karoo	<i>Stipagrostis hirtigluma</i> desert plains grasslands	127,162	3.08	110	11.6
16	Nama Karoo	<i>Calicorema capitata</i> – <i>Commiphora saxicola</i> rocky shrublands	121,039	2.93	290	17.3
17	Nama Karoo	<i>Stipagrostis hirtigluma</i> – <i>Commiphora wildii</i> stony and rocky desert grasslands	294,415	7.12	22	14.9
18	Nama Karoo Grassland zones	<i>S. uniplumis</i> eastern grasslands	35,424	0.86	42	11.7
			1,719,168	41.60		
19	Nama Karoo	<i>Euphorbia damarana</i> – <i>Calicorema capitata</i> stony and rocky desert succulent shrublands	147,598	3.57	98	15
20	Nama Karoo	<i>Euphorbia damarana</i> – <i>Stipagrostis hochstetteriana</i> northeastern dune grass- and succulent shrublands	44,448	1.08	7	7
21	Nama Karoo	<i>Stipagrostis hochstetteriana</i> eastern desert plains grasslands	182,400	4.41	30	6
22	Savanna>Nama Karoo	<i>A. reficiens</i> – <i>Colophospermum mopane</i> eastern desert plains and hills savanna transition	239,052	5.78	39	13
23	Savanna>Nama Karoo	Brandberg mountain vegetation	56,054	1.36	31	27
	Shrubland and savanna All units		669,551	16.20		
			4,132,391	100.00		

The 'n' refers to the total number of vegetation plots sampled in the respective vegetation unit, while 'spp.' refers to the mean number of species found on the 'n' 1000 m<sup>2</sup> vegetation plots.

other regions. With regard to the large scale, the annual sum of precipitation quite obviously plays a major role in shaping the observed vegetation pattern, as underlined by Fig. 6a and b.

### 3.4. The vegetation units of the new vegetation map

In the following the single vegetation units and the overall zonation (coastal zones = 35.3% surface area, grassland zones = 41.6% surface area, shrubland and savanna = 16.2% surface area, azonal units = 6.9% surface area) will be discussed. The spatial organisation of the vegetation units is presented in the new vegetation map of the Central Namib (Fig. 7).

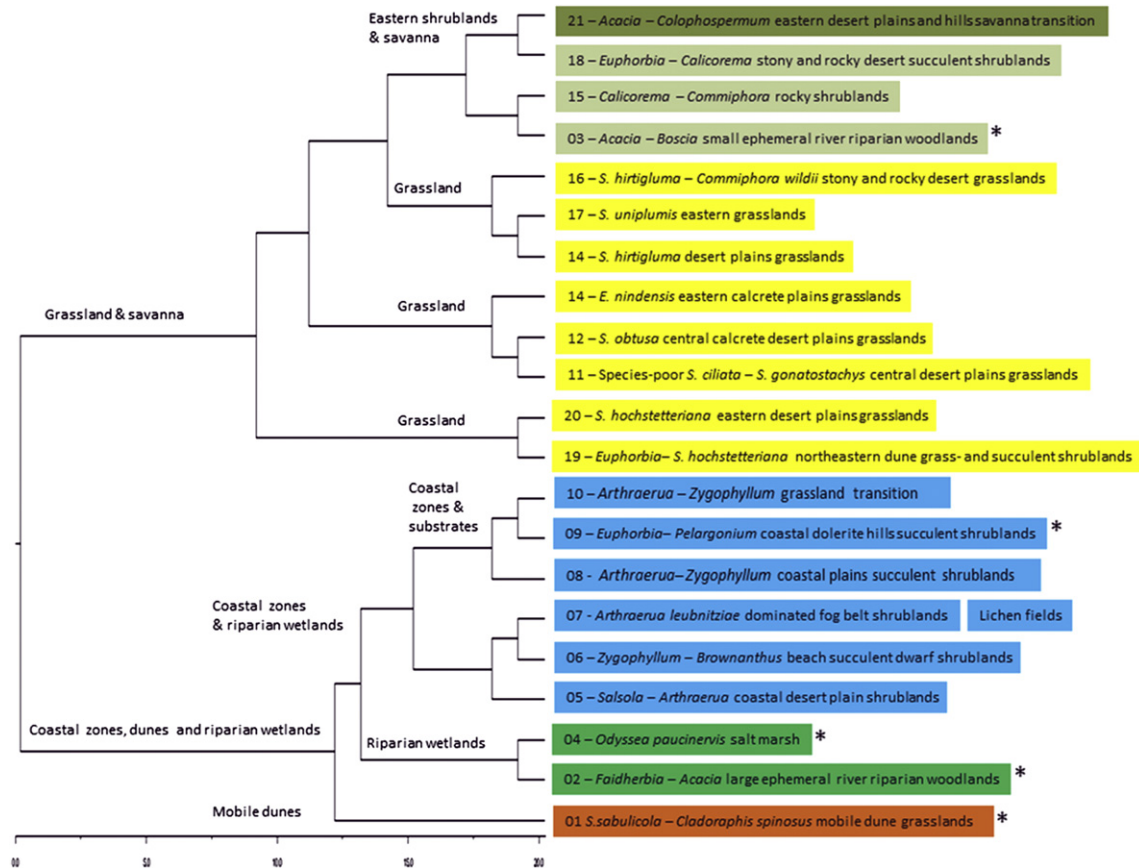
#### 3.4.1. Azonal vegetation units

**3.4.1.1. Vegetation unit 1: vegetation of mobile dune fields.** For many visitors the mobile dunes of the Namib are probably the most impressive part of the desert. The dunes place high demands on plants due to the risk of mechanical damage by sand blasting (Jürgens, 1996). Erosion and sedimentation add to the stress that plants generally face in arid regions. The vegetation of mobile dunes in the coastal region is characterized by the upright leaf-succulent Aizoaceae *Trianthema hereroensis*, a species able to comb out and take up fog water through the leaves (Seely et al.,

1977). After extensive summer rains (as observed in March 2000), the procumbent annual leaf-succulent Aizoaceae *Trianthema triquetra* may cover the coastal dunes for several months. The perennial grass *Cladoraphis cyperoides* is also well adapted to the saline fog and high air humidity combined with mild temperatures and reduced transpiration.

In a medium position between coast and inland, *T. hereroensis* characterizes the vegetation of mobile dune fields. In the higher, more exposed and more mobile parts of the linear dunes, *Stipagrostis sabulicola* forms a separate community. The grass is able to comb out fog (Louw and Seely, 1980), thereby creating a small fog oasis (Ebner et al., 2011). This oasis offers a habitat for the aggressive ant *Camponotus detritus* (Curtis, 1990), which feeds on the plant and defends it against invaders.

Towards the easternmost part of the mobile dune field, only about 5% of the surface area is formed by interlinked locally mobile dune crests. Mobile sand only occurs on the crests of these "reticulate dunes", whose highest parts are bare of any vegetation, therefore allowing percolation of water after heavy summer rains to a depth of several decimeters. The so-generated ground water resource supports several plant communities. Near the crests a belt of *S. sabulicola* occurs, followed by a community dominated by *Stipagrostis lutescens* and/or *Cladoraphis spinosus* with occasional



**Fig. 5.** Hierarchical clustering showing the similarity of vegetation units based on mean fidelity values of diagnostic species. UPGMA hierarchical clustering with Bray–Curtis distance was used to create a dendrogram from a 21-column synoptical table. The dendrogram was proportionally scaled for better visualization. Asterisks mark azonal vegetation units. In the labels, 'S.' and 'E.' code for '*Stipagrostis*' and '*Eragrostis*', respectively.

shrubs, dwarf shrubs and geophytes. Even certain tree species, in particular *Acacia erioloba*, rarely also *Parkinsonia africana*, can develop at or close to the bare crest areas.

Up to 95% of the dune valleys (sheets of aeolic sand) are inhabited by a community formed by the short-lived *S. ciliata*, more rarely also *S. obtusa* (mostly associated with calcrete crusts) accompanied by other annual grasses and herbs. In these short-lived grasslands, circular bare patches ("fairy circles") occur in large numbers. Numerous hypotheses have been proposed to explain this frequent structure. In addition to early hypotheses (for review see Van Rooyen et al., 2004), it was recently proposed that they are caused by either microseepages of geochemical gases (Naudé et al., 2011) or aggressive ants (Picker et al., 2012).

The above described mobile dune vegetation is found in the Great Namib Erg, south of the Kuiseb and, partly, in the coastal dunes between Walvis Bay and Swakopmund. It is interesting that the large consolidated dune fields north of the Brandberg (unit 20) as well as vast sand sheets north of the Chuos mountains do not share the above described species pool with the exception of some of the phreatophytes, e.g. *P. africana*.

**Diagnostic environmental characteristics:** Aeolian sands and mobile dunes.

**Diagnostic species:** *Cladoraphis spinosa*, *S. lutescens*, *S. sabulicola*, *T. hereroensis*.

**3.4.1.2. Vegetation unit 2: riparian woodlands of the large dry river beds.** The fully developed riparian woodlands of the larger ephemeral rivers (dry river beds) are characterized by trees reaching a height of 10 m and more (Huntley, 1985; Jacobson et al.,

1995; Seely and Buskirk, 1981; Theron et al., 1980). *Faidherbia albida* and *A. erioloba* are dominant in that size class, while *Combretum imberbe* and *Euclea pseudebenus* are somewhat smaller. *Salvadora persica* and *Tamarix usneoides* mostly occur as shrubs or small trees and are restricted to the margin of the river bed, with *Tamarix*, *Salvadora* and *Euclea* typically growing at greater distances from the proper river bed.

Small shrubs and perennial herbs are found beneath the shrubs and trees, sometimes also invading the proper river bed for a couple of months after good rains. Among these are *Pechuel-Loeschea leubnitziae*, *Tribulus zeyheri* and, in wet saline places, *Suaeda plumosa*, *Cyperus marginatus* and *Phragmites australis*. Sandy stretches can support perennial grassland with *Stipagrostis namaquensis* in particular in the South, while *Stipagrostis damarensis* occurs more frequently in the Northeast.

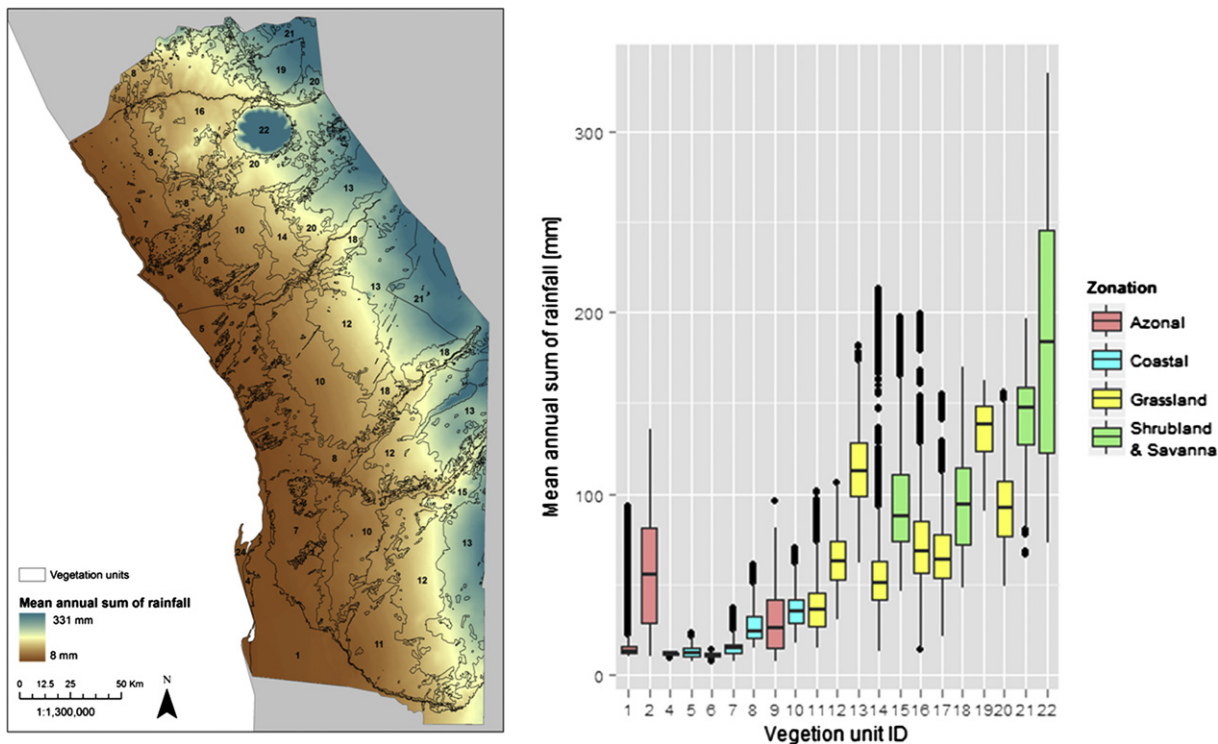
The often disturbed river habitats are easily invaded by exotic species such as *Datura innoxia*, *D. stramonium*, *Nicotiana glauca*, *Argemone ochroleuca*, *Prosopis* spp. and *Ricinus communis* (Boyer and Boyer, 1989; Henschel and Parr, 2010), which are mainly found along the large streams (Ugab, Omaruru, Khan, Swakop, Kuiseb).

**Diagnostic environmental characteristics:** Banks of large dry rivers.

**Diagnostic species:** *A. erioloba*, *D. stramonium*, *E. pseudebenus*, *F. albida*, *N. glauca*, *Pechuel-L. leubnitziae*, *R. communis*, *S. persica*, *S. plumosa*, *T. usneoides*.

**3.4.1.3. Vegetation unit 3: riparian vegetation of small dry river beds.** The smaller river beds not mappable at the scale of this study represent an important element of the Pro-Namib. They are





**Fig. 6.** Left: overlay of the vegetation units with a raster representing the spatial pattern of the mean annual sum of rainfall. The high rainfall values on top of the Brandberg are most likely an artefact caused by the WorldClim methodology. Right: boxplots showing the distribution of precipitation values for each vegetation unit. The box refers to 50% of all values. The line below the box represents the lower quartile (<25%) of the value range, the line above the box the upper quartile (>75%) of all values. The line in the box represents the median, while small black circles represent outlier values beyond the 95 percentile. Colors code for the major zonation of the Namib Desert.

conspicuous linear oases formed by trees within an otherwise open grassland or desert. River beds with sufficient storage and flux of underground water over several months have a species composition similar to that of the large river beds (excluding *F. albida*), while the cover values remain considerably lower. Typical of the small river beds are, however, small life forms. While many of these species (e.g. *A. reficiens* and *Boscia foetida*) also occur in zonal landscapes further inland, in the dryer parts of the Central Namib, they are restricted to the more humid ephemeral rivers. Generally, the riparian vegetation contains a higher, denser and woodier vegetation than the neighboring zonal landscape.

**Diagnostic environmental characteristics:** Banks of small dry rivers and minor washes.

**Diagnostic species:** *A. erioloba*, *A. reficiens*, *Blepharis gigantea*, *B. foetida*, *Grewia tenax*, *Indigofera heterotricha*, *Kissenia capensis*, *Leucosphaera bainesii*, *Petalidium setosum*, *Phaeoptilum spinosum*, *S. hochstetteriana*, *S. namaquensis*, *Stipagrostis damarana*, *S. uniplumis*, *T. zeyheri*, *Tricholaena monachne*, *Trichodesma africanum*.

**3.4.1.4. Vegetation unit 4: *Odysea paucinervis* salt marsh.** Along the coast and in the lower reaches of the large ephemeral rivers, saline loamy soils with a pH > 8 occur. Here, *O. paucinervis* can develop dense lawns, and *Lycium cinereum* can be found frequently. This vegetation unit was also described by Robinson (1976). In these species-poor communities, we found an average of only 3.5 species per 1000 m<sup>2</sup>.

**Diagnostic environmental characteristics:** loamy saline wetlands close to the coast.

**Diagnostic species:** *O. paucinervis*, *L. cinereum*, *S. nollothensis*.

**3.4.1.5. Vegetation units 23 and 24: Sandwich Harbour Lagoon and parts of Walvis Bay.** The salt marsh communities of these units

were thoroughly described by Robinson (1976). He distinguished a number of communities characterized by *Typha capensis*, *Sarcocornia natalensis*, *Sporobolus virginicus*, *Scirpus dioicus*, *P. australis* and *O. paucinervis*. The habitat of the different communities is mainly controlled by soil salinity and the extent of flooding. For this study, no relevés were sampled at Sandwhich Harbour, and therefore these units were not included in the vegetation classification. Because of the unique habitat conditions including freshwater sources and due to the quite extraordinary species combination, we keep these units separate. They are, however, related to unit 4 (*O. paucinervis* salt marshland).

**3.4.2. Coastal zones: vegetation units 5–10 (Succulent Karoo biome)**

In the following, five larger zonal units and one azonal unit are presented as a group of vegetation units. Together they form the temperate Succulent Karoo component. They include:

**Vegetation unit 5:** *S. nollothensis*–*A. leubnitziae* coastal desert plain shrubland.

**Vegetation unit 6:** *Z. clavatum*–*B. kuntzei* beach succulent dwarf shrublands Vegetation.

**Unit 7:** *A. leubnitziae*-dominated fog belt shrublands

**Vegetation unit 8:** *A. leubnitziae*–*Z. stapffii* coastal plains succulent shrublands.

**Vegetation unit 9:** *Euphorbia giessii*–*Pelargonium otaviense* coastal dolerite hills succulent shrublands (azonal unit).

**Vegetation unit 10:** *A. leubnitziae*–*Z. stapffii*–*S. ciliata* desert plains transitional succulent shrub- and grasslands.

With respect to phytogeography, these coastal units are clearly related to the Succulent Karoo region of the Greater Cape flora

**Coastal zones**

- 05 - *Salsola* – *Arthroa* coastal desert plain shrublands
- 06 - *Zygophyllum* – *Brownanthus* beach succulent dwarf shrublands
- 07 - *Arthroa* dominated fog belt shrublands
- 07 - *Arthroa* dominated fog belt shrublands with Lichen fields (a - e)
- 08 - *Arthroa* – *Zygophyllum* coastal plains succulent shrublands
- 10 - *Arthroa* – *Zygophyllum* – *S. ciliata* transitional shrub- and grasslands

**Grassland zones**

- 11 - Species-poor *S. ciliata* – *S. gonatostachys* central desert plains grasslands
- 12 - *S. obtusa* central calcrete desert plains grasslands
- 13 - *E. nindensis* eastern calcrete plains grasslands
- 14 - *S. hirtigluma* desert plains grasslands
- 16 - *S. hirtigluma* – *Commiphora* stony and rocky desert grasslands
- 17 - *S. uniplumis* eastern grasslands
- 19 - *Euphorbia* – *S. hochstetteriana* dune grass- and succulent shrublands
- 20 - *S. hochstetteriana* eastern desert plains grasslands

**Shrubland and Savanna zones**

- 15 - *Calicorema* – *Commiphora* rocky shrublands
- 18 - *Euphorbia* – *Stipagrostis* northeastern dune grass- and succulent shrublands
- 21 - *Acacia* – *Colophospermum* eastern desert plains and hills savanna transition

**Azonal units**

- 01 - *S. sabulicola* – *Cladoraphis* mobile dune grasslands
- 02 - *Faidherbia* – *Acacia* large ephemeral river riparian woodlands
- 04 - *Odysea paucinervis* salt marsh
- 09 - *Euphorbia* – *Pelargonium* coastal dolerite hill succulent shrublands
- 22 - Brandberg mountain vegetation
- 23 - Sandwich Harbour Lagoon
- 24 - Walvis Bay (urban area and Pelican Point)

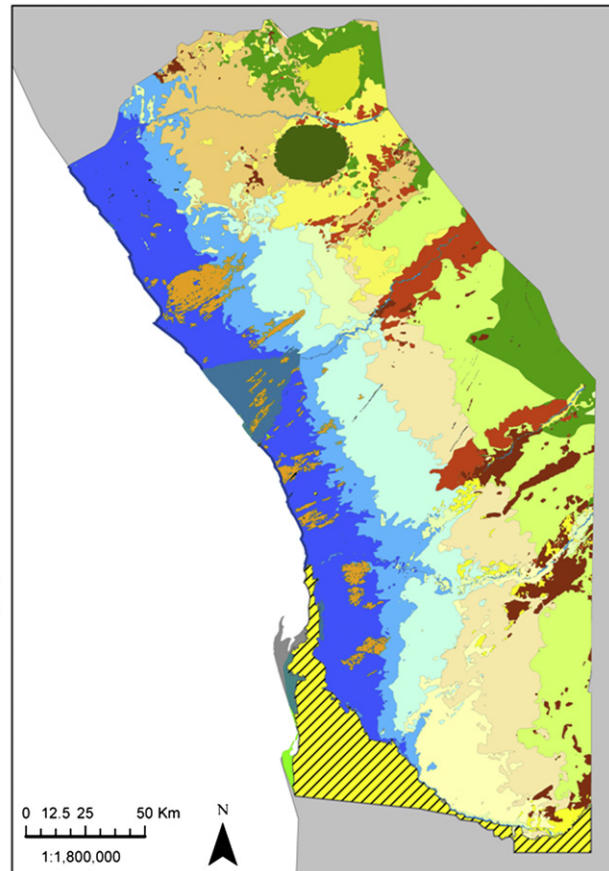


Fig. 7. New vegetation map of the Central Namib. In the labels, 'S.' and 'E.' code for '*Stipagrostis*' and '*Eragrostis*', respectively. A modified print version of this map and a KMZ are available at the BIOTA-AFRICA website: URL: <http://www.biota-africa.org/downloads/cnvegmap.zip>.

(Jürgens, 1991). The mild temperatures and the high relative air humidity caused by the Benguela Upwelling system provide conditions quite similar to the core area of the Succulent Karoo biome, which is located at higher latitudes in the Sperrgebiet, in Namaqualand and in parts of the Karoo, there typically combined with winter rainfall seasonality. Additional moisture is frequently provided by fog and dew, which is also the case in the coastal parts of the winter rainfall region further south.

The plants' uptake of water from fog and other sources has been studied intensively. A review of relevant papers is presented in this special issue in the article of Eckardt dealing with various aspects of moisture (Eckardt et al., this issue). Succulents, and here especially 27 species of leaf succulents many of which are CAM plants, occur with high cover values. Numerous articles have shown that leaf succulents are well adapted to arid regions which offer mild temperatures, high air humidity and predictable availability of (small) amounts of water (summary in Von Willert et al., 1991).

**3.4.2.1. Vegetation unit 5: *S. nollothensis*–*A. leubnitziae* coastal desert plain shrubland.** This unit is largely restricted to the sediment fan near the mouth of the Omaruru River. Here, access to ground water of the Omaruru supports the growth of large shrubs of *S. nollothensis*, occasionally accompanied by *A. leubnitziae*. Strong coastal winds shape the plants, and sand piled up around the plant individuals forms large microdunes of several meters in diameter accumulating organic matter. After rains *Mesembryanthemum hypertrophicum*, *Mesembryanthemum guerichianum*, *Galenia papulosa*, *Galenia africana* and *Aizoanthemum galenioides* can form a dense succulent therophytic vegetation layer.

**Diagnostic environmental characteristics:** low amounts of rainfall, wind-swept open plains with sand transport and sand blasting, low temperatures, mainly surficial saline deposits (gravel, etc.), intense fog input, flat terrain, low ruggedness, equal distribution of solar energy as reflected by the diurnal anisotropic heating (DAH) parameter (Table 1).

**Diagnostic species:** *A. leubnitziae*, *S. nollothensis*.

**3.4.2.2. Vegetation unit 6: *Z. clavatum*–*B. kuntzei* beach succulent dwarf shrublands.** The *Z. clavatum*–*B. kuntzei* beach dwarf shrubland community is a highly specialized community, which grows directly on the beach, forming the first line of plant life, or just a few hundred meters inland in case of very flat beaches. Both diagnostic species develop tussocks with a very dense surface. The stable structure of these tussocks is essential for the occurrence of other organisms.

**Diagnostic environmental characteristics:** Sandy habitats directly at the beach or a few hundred meters inland.

**Diagnostic species:** *A. leubnitziae*, *B. kuntzei*, *Mesembryanthemum cryptanthum*, *Z. clavatum*.

**3.4.2.3. Vegetation unit 7: *A. leubnitziae*-dominated fog belt shrublands.** *A. leubnitziae* can form monodominant stands on slopes and on top of flat elevations. Occasionally it also occurs in valley-like depressions, proper river environments and pan-like depressions. Nearly always, *A. leubnitziae* is associated with foamy topsoils which are often formed underneath deflation plasters and/or above gypcretes. In all habitats the species may be associated with *A. galenioides*, *B. kuntzei*, *Drosanthemum paxianum*, *Jamesbrittenia*

*maxii*, *M. cryptanthum*, *Psilocaulon subnodosum*, *Senecio engleranus*, *Stipagrostis hermannii*, *Tetragonia reduplicata* and *Zygophyllum spongiosum*. In shallow drainage lines, populations of *W. mirabilis* are found, some of them in less than 11 km distance from the coast.

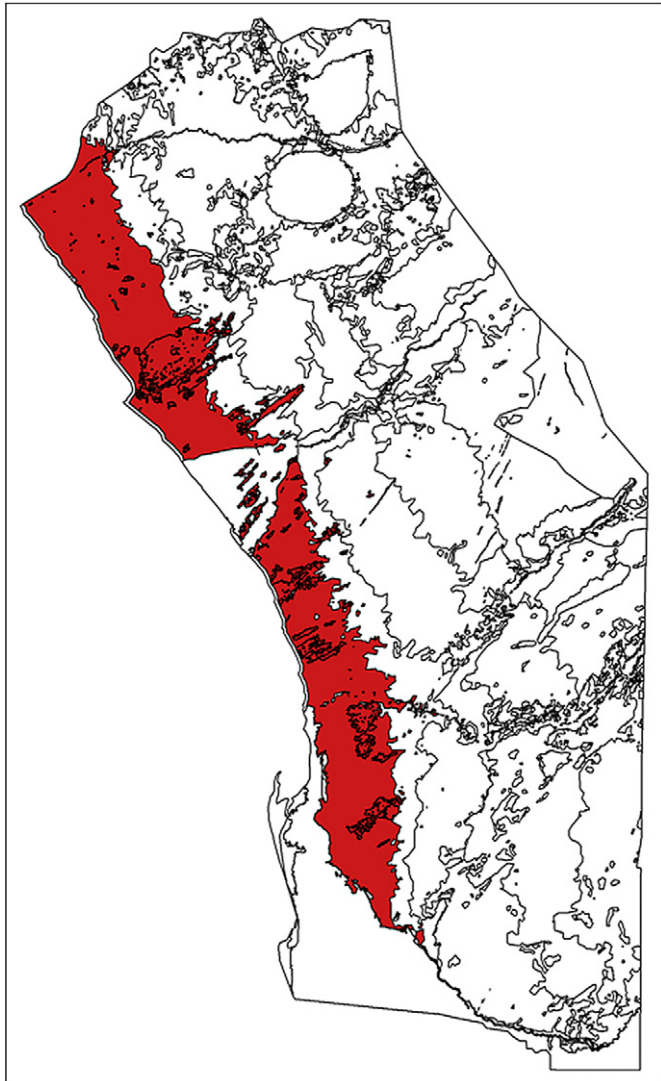
If soils are extremely saline, the contribution of *A. leubnitziae* to the vegetation cover decreases while that of *M. cryptanthum* and *Z. spongiosum* increases. In extreme cases *A. leubnitziae* is completely replaced by these saline species.

**Diagnostic environmental characteristics:** typical environmental characteristics include low amounts of rainfall, low temperatures, mainly surficial deposits (gravel, etc.), intense fog input, flat terrain, low ruggedness, equal distribution of solar energy (DAH).

**Diagnostic species:** *A. leubnitziae*, *S. hermannii* (Fig. 8).

**3.4.2.4. Vegetation unit 7a: *A. leubnitziae* fog belt shrublands with fruticose lichen zones. Coastal subtype:** located on fine coastal gravel flats with stabilized soils. *Teloschistes capensis* forms large mats on more sandy and unstable or softer patches. Although these sandy patches show an overall low lichen cover, scattered quartz pebbles are colonized by saxicolous lichen species (Schultz, 2006).

**Inland subtype:** this subtype is limited to the undulating coarse quartz gravel plains in the hinterland of the northern part of the



**Fig. 8.** Distribution of vegetation unit 7 *Arthroa leubnitziae*-dominated fog belt shrublands and lichen fields (a–e).

study area, where high amounts of fog precipitation have led to the development of an extremely species-rich community of both terricolous and saxicolous lichens. *T. capensis* is abundant but does not form large mats. Additionally, the foliose *Xanthoparmelia walteri* occurs frequently alongside with scattered thalli of *Xanthomaculina convoluta* and *Xanthomaculina hottentotta* as well as abundant genera of *Acarospora*, *Buellia*, *Caloplaca*, *Lecidea*, *Lecidella* and *Neofuscelia*.

**3.4.2.5. Vegetation unit 7b: *A. leubnitziae* fog belt shrublands with fruticose–foliose lichen zone. Coastal subtype:** the *T. capensis*, *X. walteri*, *Neofuscelia namaensis* quartz desert community is located on bright quartz gravel plains (Schultz, 2006). As these territories are interspersed with numerous sandy washes. They are more undulating than the gravel plains typical for the previous community. Both *T. capensis* and *N. namaensis* separate this community from other lichen communities in the central Namib Desert. Under dry conditions, high abundances of *X. walteri* and *N. namaensis* result in a black color clearly distinguishable from the bright quartz gravel plains. Fruticose and foliose lichen species dominate in this community. Additionally, a variety of saxicolous species occur on quartz pebbles. Thalli of terricolous *Caloplaca volkii* and *Lecidella crystallina* grow scattered, but dominate the crustose share on gypsum-rich soils.

**Inland subtype:** the composition of this community resembles the inland subtype of unit 7a. It differs with respect to the low abundance of the fruticose *T. capensis* species in favour of foliose species such as *X. walteri* and *X. hottentotta*.

**Mountainous subtype:** examples of this mountainous community occur on elevated yet strongly eroded outcrops or dolerite ridges of the Central Namib. Despite the occurrence of the accompanying fruticose species *T. capensis*, *Ramalina* spp. and *Santessonia* spp., this mountainous community is distinguished by high abundances of the foliose lichen *X. hottentotta* (Wessels, 1989). In some localities, this species forms almost pure stands. Typically, however, this community occurs on rocky ridges and mountains together with *X. walteri* and *N. namaensis*. Several crustose lichen species may also occur in variations of this community.

**3.4.2.6. Vegetation unit 7c: *A. leubnitziae* fog belt shrublands with foliose lichen zones. Quartz gravel subtype:** ample examples of this lichen community occur east of the town of Henties Bay on the vast quartz gravel plains of the Omaruru River (Schultz, 2006). This type of lichen community is characterized by almost pure stands of the foliose lichen *X. walteri* combined with the terricolous species *C. volkii* and *L. crystallina*. As these sand-binding species also stabilize the quartz pebble surface layer, their abundance triggers the saxicolous growth of *X. walteri*. Where coarse gravel is predominant, interspersed occurrences of *Caloplaca namibensis*, *Caloplaca elegantissima* and *Neofuscelia* spp. can be found.

**Mountainous subtype:** this subtype is dominated by the foliose species of *X. walteri* and accompanied by scattered occurrences of *X. hottentotta* as well as *Neofuscelia*, *Buellia* and *Paraparmelia* species. It is most often found on the almost entirely closed layer of fine to medium dark gravel material covering the substrates in the northern part of the study area. This dark gravel material is quite different from the otherwise quartz gravel-covered plains or gypsum substrates typical for the central Namib Desert. As it is only loosely embedded in an otherwise sandy substrate, saxicolous growth forms prevail in this community. Sand-binding species of *C. volkii* and *L. crystallina* occur only interspersed where the gravel cover is disturbed.

**3.4.2.7. Vegetation unit 7d: *A. leubnitziae* fog belt shrublands with foliose crustose lichen zones. Quartz gravel subtype:** in its species

composition, this community resembles the *X. walteri* community of the fine quartz gravel plains of unit 7c (Schultz, 2006). Thus it is considered a transition between communities either dominated by foliose or by crustose species. The unit includes the sand-binding terricolous species *C. volkii* and *L. crystallina*, which both occur in lower abundances. Also, *X. walteri* is less frequent. In contrast, the saxicolous growth types of *C. namibensis*, *C. elegantissima* and *Neofuscelia* spp. are more abundant due to a better adaptation to the increased corrosion in these localities.

**Mountainous subtype:** characterized by an abundant saxicolous growth of foliose *X. walteri* and crustose *C. elegantissima*, the large, dark rock debris are almost fully overgrown in this unit. Within the study area, this subtype is mainly limited to the strongly eroded outcrops or dolerite ridges of the Central Namib, but also covers large parts of the coastal rock debris areas near the Huabmond. Less abundant crustose species of this community are *C. namibensis*, *Neofuscelia* spp., *Buellia* spp. and *Paraparmelia* spp.

**Gypsum subtype:** terricolous species of *C. volkii*, *L. crystallina* and foliose *X. convoluta* build this community, which covers the surface to almost 100%. Here, *X. walteri* is strikingly more abundant than in the crustose community of the gypsum plains. Scattered *T. capensis* tufts occur together with *Ramalina* spp. The unit is mainly limited to the coarse gravel hummocks of the southern parts of the study area where it represents the most diverse lichen community. Several other crustose species of *Arcarospora*, *Buellia*, *Caloplaca*, *Diplochistes* and *Lecidea* also occur subordinately.

**3.4.2.8. Vegetation unit 7e: *A. leubnitziae* fog belt shrublands with crustose lichen zones. Quartz gravel subtype:** predominantly crustose lichen species are present in this community. Various *Caloplaca*, *Lecidella*, *Buellia*, *Neofuscelia*, *Lecidea* and *Paraparmelia* species are found, growing saxicolously on fine quartz gravel. Interspersed coarse quartz gravel is often covered by *X. walteri*. Where the gypsum substrate is not entirely covered by quartz gravel, *L. crystallina* and *Acarospora* species also become abundant (Schultz, 2006).

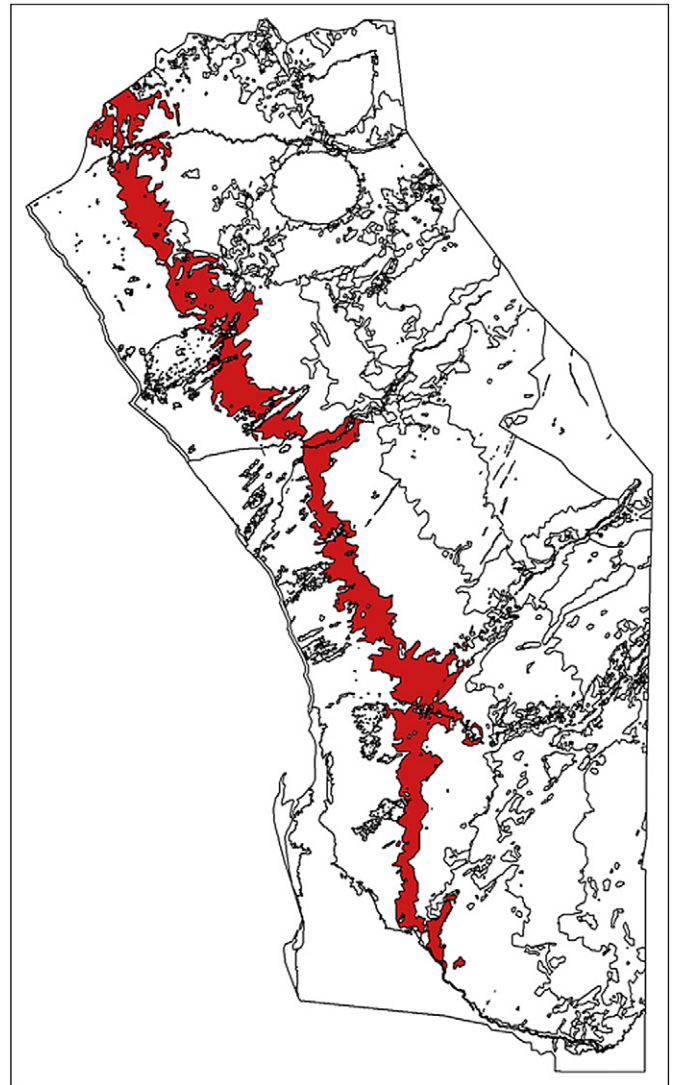
**Gypsum subtype:** an abundant cover of *C. volkii*, *L. crystallina* (both terricolous species) and *X. convoluta* (vagrant) characterizes this community. Occasionally, lichen thalli cover nearly 100% of the soil surface, clearly dominating this community. Through their sand-binding ability, these soil crust lichen species strongly contribute to the stabilization of the otherwise only semi-stable soil surface. In between, there are scattered occurrences of foliose and fruticose species such as *X. walteri* and *T. capensis*. Several species of *Arcarospora*, *Buellia*, *Caloplaca*, *Diplochistes* and *Lecidea* occur subordinately.

**3.4.2.9. Vegetation unit 8: *A. leubnitziae*–*Z. stapffii* coastal plains succulent shrublands.** In unit 8, located adjacent to unit 7, the proportion of *Z. stapffii* increases towards the inland. Over wide stretches *A. leubnitziae* and *Z. stapffii* co-occur as the only two conspicuous species. To the West single species characteristic for the previous *A. leubnitziae* unit (unit 7) may also occur. To the North, close to Goboboseberge and Messum Crater, *W. mirabilis* adds to the unit, growing in shallow drainage lines.

**Diagnostic environmental characteristics:** similar to unit 7, but with higher temperatures and twice the average annual precipitation.

**Diagnostic species:** *A. leubnitziae*, *S. subacaulis*, *Z. stapffii* (Fig. 9).

**3.4.2.10. Vegetation unit 9: *E. giessii*–*P. otaviense* coastal dolerite hills succulent shrublands.** Although similar to the *A. leubnitziae*–*Z. stapffii* unit (unit 8), this unit exhibits a notably higher species richness with *Aloe asperifolia*, *B. kuntzei*, *E. giessii*, *Euphorbia lignosa*, *Heliotropium oliveranum*, *Hoodia pedicellata*, *Kleinia longiflora*,



**Fig. 9.** Distribution of vegetation unit 8 *Arthroa leubnitziae*–*Zygophyllum stapffii* coastal plains succulent shrublands.

*P. otaviense*, *Sarcocaulon marlothii*, *Tetragonia reduplicate*, *Aizoanthemum membrumconnectens*, *Eberlanzia sedoides*, *Sesuvium sesuvioides* and *Tripteris microcarpa*.

Evolved in the peculiar environment of dolerite ridges, this plant community stretches from 4 to about 45–50 km inland. Further inland it is replaced by the *Calicorema capitata*–*Commiphora saxicola* community. The elevation of the specific basaltic rock (dolerite) and its fragmentation into large blocks offer various microhabitats suitable for a co-existence of the above-listed species. Some of the dolerite ridges also form habitat corridors serving as bridges/connections between isolated dolerite ridges. The longest dolerite ridges stretch over a length of 150 km.

**Diagnostic environmental characteristics:** dolerite ridges from the coast to about 50 km inland.

**Diagnostic species:** *A. asperifolia*, *A. leubnitziae*, *B. kuntzei*, *E. giessii*, *E. lignosa*, *H. pedicellata*, *K. longiflora*, *P. otaviense*, *S. marlothii*, *T. reduplicata*, *Z. stapffii*.

**3.4.2.11. Vegetation unit 10: *A. leubnitziae*–*Z. stapffii*–*S. ciliata* desert plains transitional succulent shrub- and grasslands (ecotone between Succulent Karoo and Nama Karoo).** The Succulent Karoo elements

decrease between 30 km and 50 km inland (a bit further inland at the dolerite ridges). This transition zone is characterized by a decrease of *Z. stapffii* and an increase of *S. ciliata* and *C. saxicola* towards the East. *Monechma cleomoides*, *Asparagus pearsonii* and *Adenolobus pechuelii* also occur with high frequencies. The well-known Welwitschiavlakte population of *W. mirabilis* is located within this unit.

**Diagnostic environmental characteristics:** high values of isothermality (ratio of monthly versus annual temperature range, a measure of temperature stability); higher temperatures with more rainfall and similar topology and geology as units 6, 7 and 8.

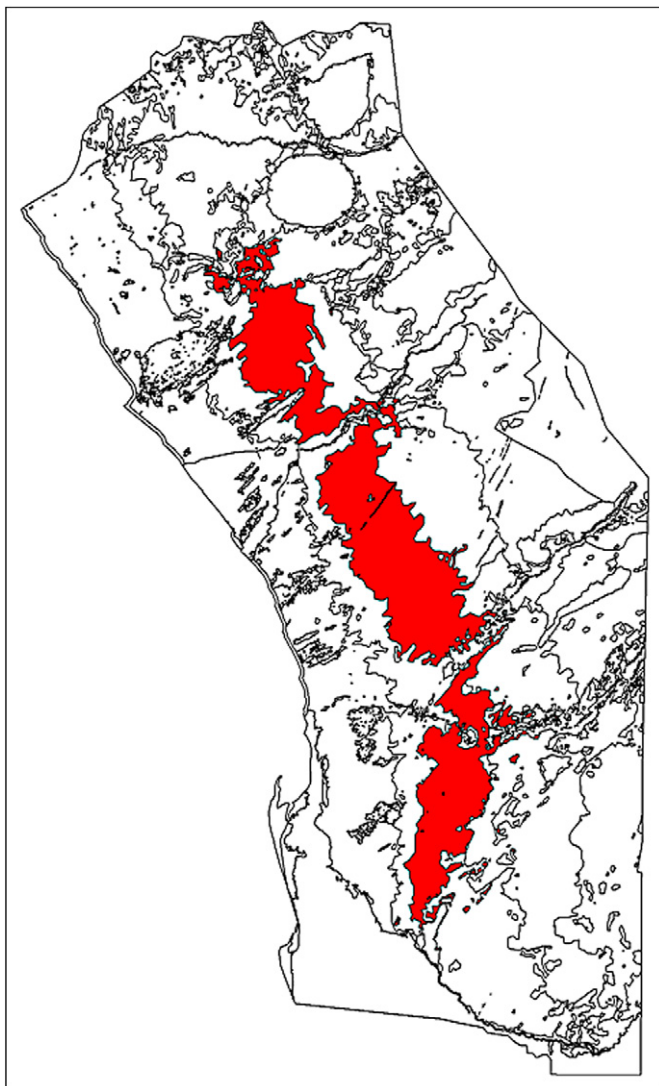
**Diagnostic species:** *A. pearsonii*, *S. sesuvioides*, *S. ciliata*, *Z. stapffii* (Fig. 10).

### 3.4.3. Grassland zone (Nama Karoo biome)

In the following, eight large zonal units are presented as a group. Together they form the grassland component (Nama Karoo biome) of the Central Namib. They include:

**Vegetation unit 11:** Species-poor *S. ciliata*–*S. gonatostachys* central desert plains grasslands.

**Vegetation unit 12:** *S. obtusa* central calcrete plains grasslands.



**Fig. 10.** Distribution of vegetation unit 10 *Arthroa leubnitziae*–*Zygophyllum stapffii*–*Stipagrostis ciliata* desert plains transitional succulent shrub- and grasslands.

**Vegetation unit 13:** *E. nindensis* eastern calcrete plains grasslands.

**Vegetation unit 14:** *S. hirtigluma* desert plains grasslands.

**Vegetation unit 16:** *S. hirtigluma*–*Commiphora wildii* stony and rocky desert grasslands.

**Vegetation unit 17:** *S. uniplumis* eastern grasslands.

**Vegetation unit 19:** *E. damarana*–*S. hochstetteriana* northeastern dune grass- and succulent shrublands.

**Vegetation Unit 20:** *S. hochstetteriana* eastern desert plains grasslands.

The grassland units make up the largest surface proportion of all zones (1,719,168 ha = 41.6% of the study area, Table 2). More research is needed on the spatially very important grasslands, in particular as these grasslands are highly productive for a desert ecosystem. They also influence food networks and transport biomass by wind into neighboring ecosystems. The grass census initiated at Gobabeb established evidence on the relationship between precipitation and biomass production (Günster, 1993; Seely, 1978). It provides baseline knowledge on minimum rainfall requirement for germination and establishment of annual (ca. 10 mm) and of perennial tussocks (ca. 25 mm) of *S. ciliata*.

In the Central Namib, there are many grasses using the C4 photosynthetic pathway (Vogel and Seely, 1977); however, there also is an astonishing number of plants from other families using C3 carboxylation. Schulze et al. (1996) showed that the grass flora of Namibia (374 species in 110 genera; mainly C4 photosynthetic pathway) shows surprisingly little variation in  $\delta^{13}\text{C}$  values along a rainfall gradient (50–600 mm) and in different habitat conditions, in spite of strong  $\delta^{13}\text{C}$  differences between metabolic types.

**3.4.3.1. Vegetation unit 11: species-poor *S. ciliata*–*S. gonatostachys* central desert plains grasslands.** Numerous vegetation records nearly exclusively consist of either of the two grasses *S. ciliata* or *S. gonatostachys* (often with the annual leaf-succulent *Z. spongiosum*).

Next to some areas of units 7, 8 and 10, these desert plains represent the most species-poor parts of the central Namib Desert. Cover values are also low, in particular in the southern part (south of the Khan river valley). Together with unit 17, this unit is the species-poorest of all grassland units, with an average of 5.9 species on 1000 m<sup>2</sup> (Table 2).

**Diagnostic environmental characteristics:** warmer and wetter in comparison to units 6, 7, 8 and 10, yet still below 100 mm rainfall per annum. Flat terrain of mainly surficial deposits.

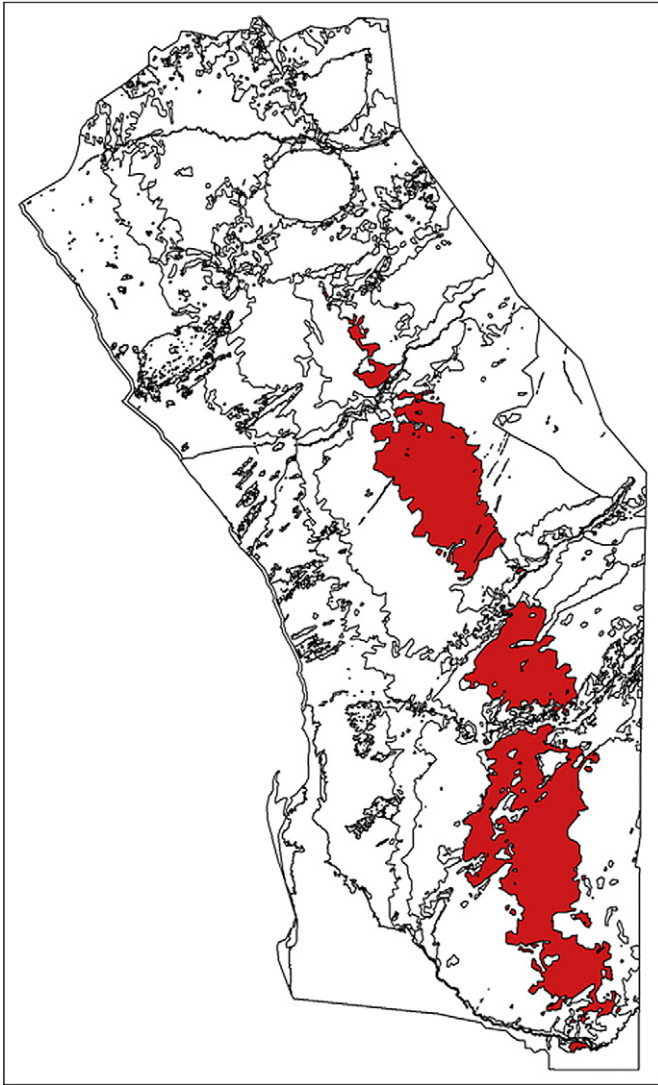
**Diagnostic species:** *S. ciliata*, *S. gonatostachys*.

**3.4.3.2. Vegetation unit 12: *S. obtusa* central calcrete plains grasslands.** The *S. obtusa* central grassland forms part of the various subunits of tropical desert margin grasslands. Inland of vegetation unit 10 (*A. leubnitziae*–*Z. stapffii*-grassland transition) and partly inland of vegetation unit 12 (*S. ciliata*–*S. gonatostachys* central desert plains), gypsum crusts and sandy areas are replaced by calcretes with a dominance of *S. obtusa*. Only *S. ciliata* and *Z. spongiosum* and, to a lesser extent, *Euphorbia phylloclada* and *S. sesuvioides* are associated with this unit. They occur only south of the Brandberg and are well established mainly south of the Omaruru River.

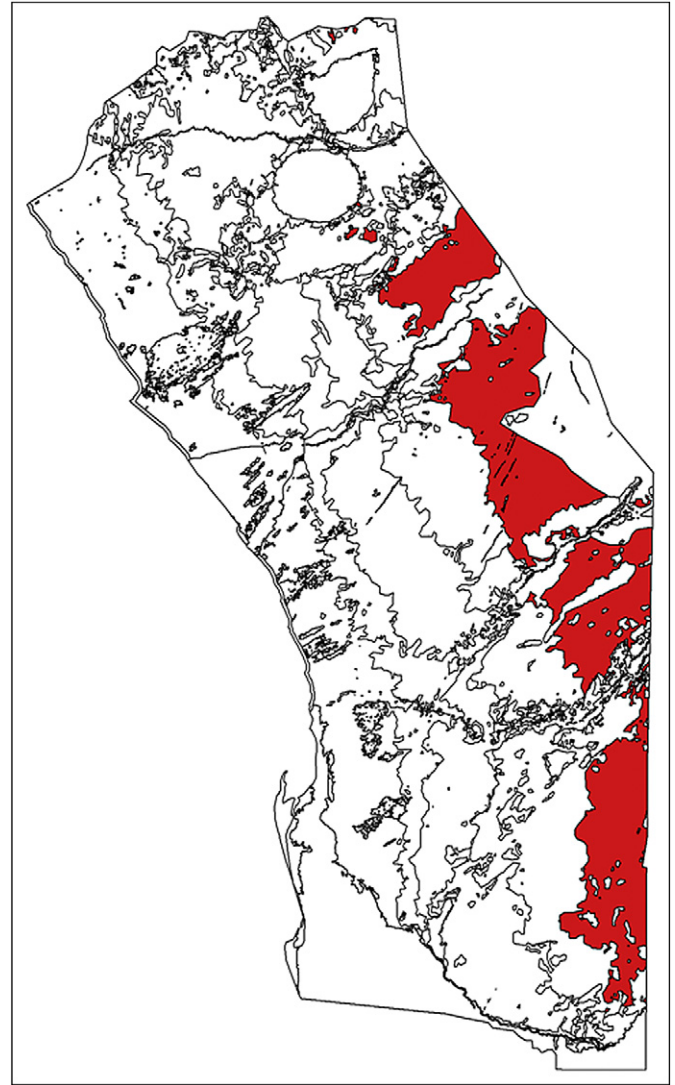
**Diagnostic environmental characteristics:** highest isothermality values, higher rainfall and temperatures in comparison to units 6–11. The terrain is still flat with predominantly surficial deposits.

**Diagnostic species:** *S. ciliata*, *S. obtusa* (Fig. 11).

**3.4.3.3. Vegetation unit 13: *E. nindensis* eastern calcrete plains grasslands.** Similar to the *S. obtusa* unit, the *E. nindensis* eastern calcrete grasslands occur on calcrete soils. Within the Central Namib, this is the most important and most extensive unit of all



**Fig. 11.** Distribution of vegetation unit 12 *Stipagrostis obtusa* central calcrete desert plains grasslands.



**Fig. 12.** Distribution of vegetation unit 13 *Eragrostis nindensis* eastern calcrete plains grasslands.

Nama Karoo grasslands. *E. nindensis* is associated with *Zygophyllum cylindrifolium*, *S. ciliata*, *S. obtusa*, *S. hirtigluma*, *Enneapogon desvauxii*, *Blepharis grossa*, *M. cleomoides*, *P. setosum*, *Geigeria alata* and others. Also local endemics such as *Tribulocarpus dimorphanthus* occur within this unit.

**Diagnostic environmental characteristics:** high isothermality values, considerable rainfall amounts; one of the warmest units. Very high Enhanced Vegetation Index (EVI) values, partly higher than those of the savanna transition unit 21. Topography is still flat with predominantly surficial deposits.

**Diagnostic species:** *E. desvauxii*, *E. nindensis*, *Geigeria ornativa*, *Oropetium capense*, *S. obtusa*, *Z. cylindrifolium*, *Z. spongiosum* (Fig. 12).

**3.4.3.4. Vegetation unit 14: *S. hirtigluma* desert plain grasslands.** Towards the northern parts of the study area, grasslands are not dominated by *S. ciliata*, *S. gonatostachys* or *S. obtusa* anymore; instead, *S. hirtigluma* prevails. This type of grassland is poorer with regard to species number and cover values in comparison to the *E. nindensis* unit (unit 13).

**Diagnostic environmental characteristics:** highly variable in rainfall and temperature. Predominantly low rainfall amounts, but high temperatures due to dark surficial deposits. Considerable values for

the vector ruggedness measure (VRM) and a large spread of diurnal anisotropic heating (DAH) values indicate a mostly undulating terrain. In the center of the unit, there is a large flat terrain.

**Diagnostic species:** *S. hirtigluma* (Fig. 13).

**3.4.3.5. Vegetation unit 16: *S. hirtigluma*–*C. wildii* stony and rocky desert grasslands.** In the very North of the study area, the generally sparse grasslands (units 11, 13 and 15) become even more sparse. They are composed of *S. hirtigluma* ssp. *hirtigluma* and *S. uniplumis* var. *intermedia*. Only after sufficient rains is it possible to determine the relative presence of these two annual grasses. Thus, we distinguish only one large unit in which the geology differs considerably. In major parts of this unit, the grassland is very sparse. Another characteristic is the sparse occurrence of *W. mirabilis* in depressions and drainage lines, while *C. wildii* is found on rocky outcrops (Fig. 14).

**Diagnostic environmental characteristics:** geologically predominantly meta-greywacke (geological class 72); strong topological heterogeneity (VRM & DAH); rainfall is very variable; minimum temperatures in the coldest month are constantly high.

**Diagnostic species:** *Boerhavia deserticola*, *Chascanum pumilum*, *Cleome suffruticosa*, *C. saxicola*, *Commiphora virgata*, *C. wildii*,

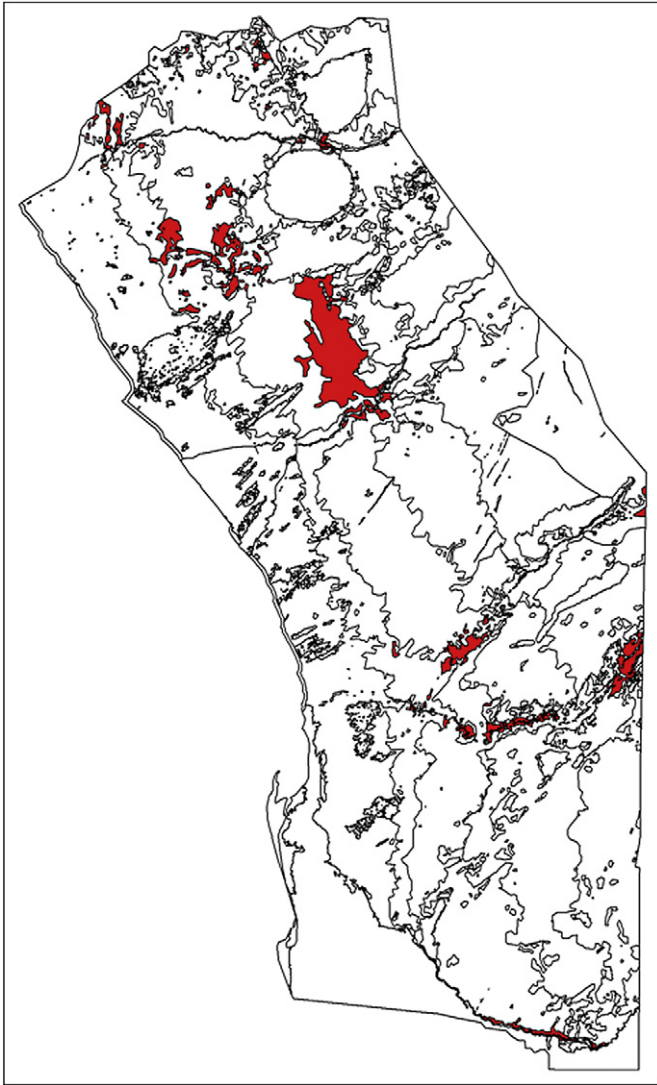


Fig. 13. Distribution of vegetation unit 14 *S. hirtigluma* desert plains grasslands.

*Crotalaria podocarpa*, *Dipcadi viride*, *Euphorbia glanduligera*, *Forskaolea viridis*, *G. alata*, *Gisekia africana*, *Hermannia helianthemum*, *Limeum argute-carinatum*, *Limeum dinteri*, *Mollugo cerviana*, *M. cleomoides*, *Pegolettia pinnatilobata*, *Petalidium canescens*, *Petalidium variabile*, *Sesamum capense*, *S. uniplumis*, *Talinum caffrum*, *Tephrosia dregeana*, *T. microcarpa* (Fig. 15).

3.4.3.6. *Vegetation unit 17: S. uniplumis eastern grasslands.* The *S. uniplumis* eastern grassland belongs to the various subunits of the desert margin grasslands. Its spatial extension is very limited, and only few species are associated with this unit. The *S. uniplumis* grassland is typically found near small rivers or close to rocky outcrops.

*Diagnostic environmental characteristics:* high rainfall amounts and mean temperatures, yet with some of the lowest minimum temperatures. High topological variability. Geology consists mainly of mica schist (class 44 in geology raster).

*Diagnostic species:* *Commiphora glaucescens*, *Pegolettia senegalensis*, *P. canescens*, *S. marlothii*, *S. uniplumis* (Fig. 16).

3.4.3.7. *Vegetation unit 19: E. damarana–S. hochstetteriana north-eastern dune grass- and succulent shrublands.* A very unique vegetation unit has developed in a dune field northeast of the

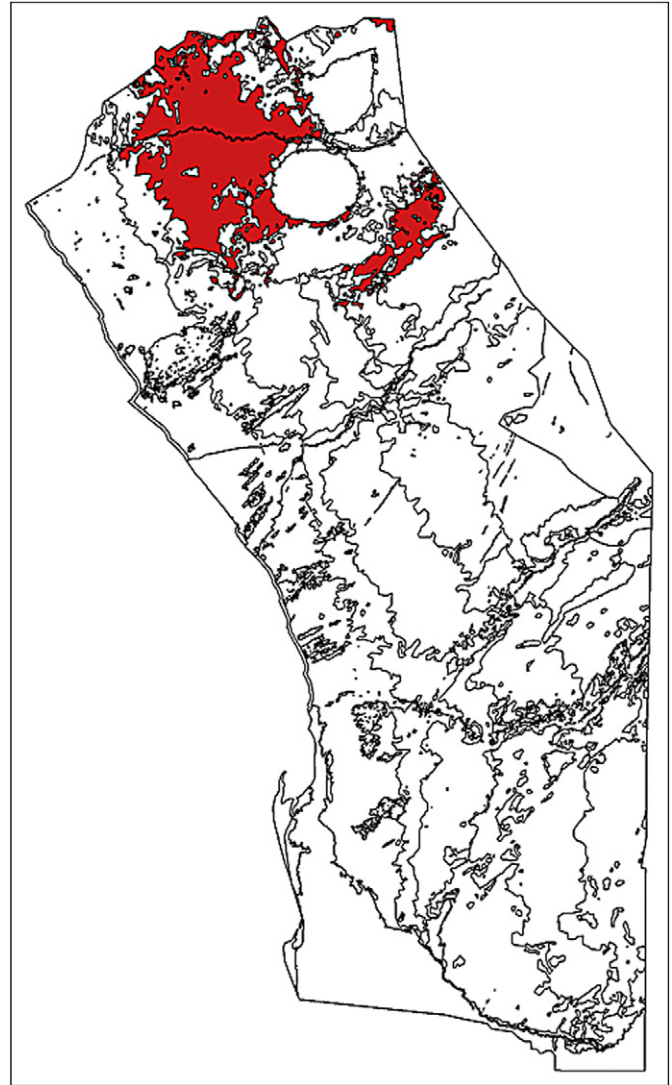


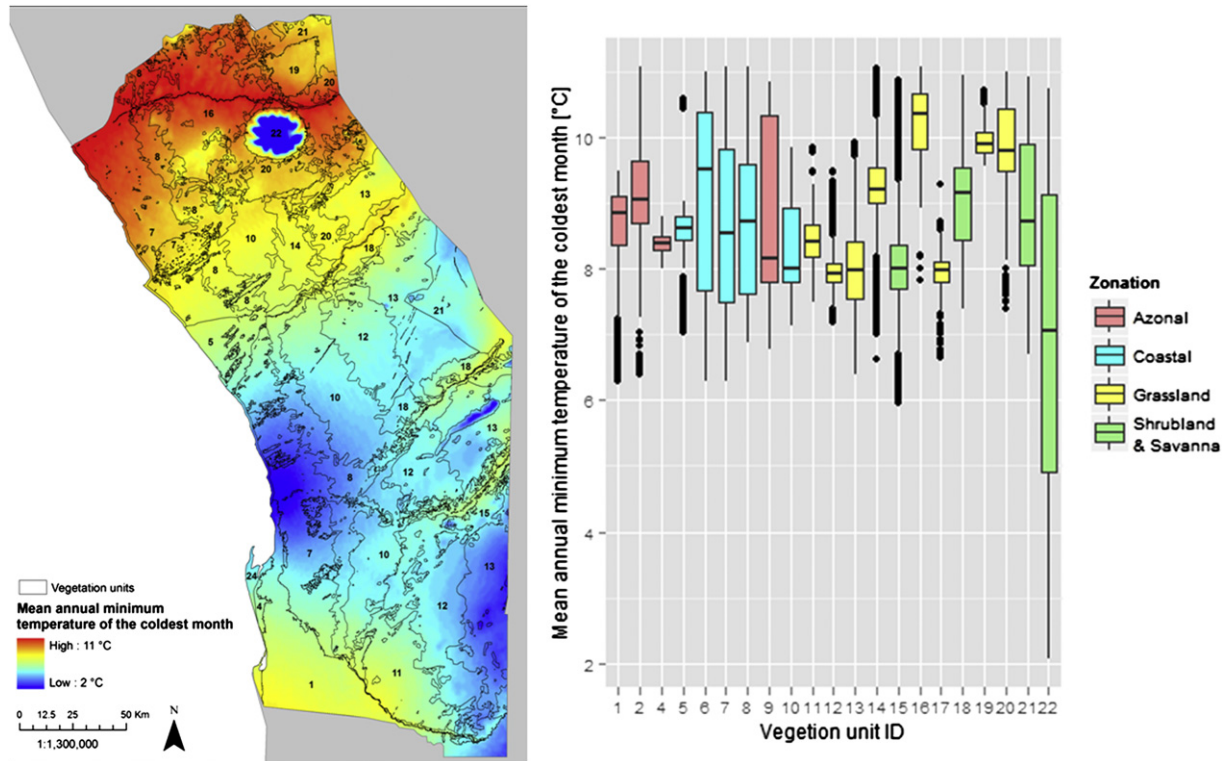
Fig. 14. Distribution of vegetation unit 16 *S. hirtigluma–Commiphora wildii* stony and rocky desert grasslands.

Brandberg. Here, *E. damarana* grows within a dense *S. hochstetteriana* grassland. Interestingly, here this stem-succulent species even occurs on partly deep sand, which is a very unusual habitat for *E. damarana*. Typically, the plant prefers shallow soils or rocky surfaces.

As the wide sand fields could only be visited once during this study, no final conclusions regarding endemism and conservation value can be drawn based on the limited number of relevés. We are, however, inclined to think that this unit is of high conservation value.

*Diagnostic species:* *A. reficiens*, *Blepharis obmitrata*, *Citrullus ecirrhosus*, *Commiphora pyracanthoides*, *Corallocarpus welwitschii*, *E. damarana*, *Harpagophytum procumbens*, *P. africana*, *Schmidtia kalahariensis*, *Stipagrostis giessii*, *S. hochstetteriana*.

3.4.3.8. *Vegetation unit 20: S. hochstetteriana eastern desert plain grasslands.* The *S. hochstetteriana* eastern grassland forms part of the various subunits of tropical desert margin grasslands. It is dominant on sandy soils close to and east of the Brandberg. Like within the other arid grasslands, species richness is limited, i.e. a mean species richness of six species per 1000 m<sup>2</sup> (Table 2).



**Fig. 15.** *Left:* spatial representation of the raster data set 'minimum temperature of the coldest month [°C]', illustrating the higher temperatures in unit 16. Small numbers within the vegetation unit polygons refer to the number of the vegetation units. *Right:* boxplots showing the distribution of temperature values for each vegetation unit. Colors code for the major zonation of the Namib Desert.

*Diagnostic environmental characteristics:* one of the brightest units with regard to the RGB Geocover Landsat image; temperature and rainfall amounts constantly high. The topography is rather flat.

*Diagnostic species:* *S. hochstetteriana* (Fig. 17).

#### 3.4.4. Shrubland and savanna zones (Nama Karoo and thornbush savanna biome)

In the following, three large units are presented as a group. Together they form the shrubland component (Nama Karoo biome) and the transition to the savanna biome. They include:

*Vegetation unit 15:* *C. capitata*–*C. saxicola* rocky shrublands (Nama Karoo biome).

*Vegetation unit 19:* *E. damarana*–*C. capitata* stony and rocky desert succulent shrublands (Nama Karoo biome).

*Vegetation unit 21:* *A. reficiens*–*C. mopane* eastern desert plains and hills savanna transition (Thornbush savanna biome).

The transition from the proper grassland to a region with an increasing importance of shrubs and finally small trees is related to the environmental gradients of increasing rainfall and increasingly stony and rocky soils. (However, within the more eastern grassland units 14–20, dwarf shrub species and shrubs species do also occur.)

The dwarf shrubs and annual species of these units have developed quite different strategies with regard to soil seed banks (Burke, 1994a) and phenological niche differentiation (Burke, 1994b). Serotinous species (e.g. *B. grossa*, *G. alata*, *G. ornativa* and *P. setosum*) possess aerial seed banks (Burke, 1992, 1994c), and some species show seed heteromorphism (Burke, 1995).

Units 15 and 18 prefer shallow soils above rock (*C. capitata*–*C. saxicola* rocky shrublands) or rocky landscapes (Vegetation unit

18: *E. damarana*–*C. capitata* stony and rocky desert succulent shrublands).

Different types of inselbergs occur scattered within these units. Their floristic composition depends on the type of rock (often either granite or dolerite) with different relationships to surrounding landscapes and mountain habitats (Burke, 2003). On these inselbergs and on the escarpment, desiccation-tolerant poikilohydric plants, e.g. *Myrothamnus flabellifolius*, inhabit rock surfaces. The results of studies on desiccation tolerance have been summarized by Moore et al. (2006). Among other hypotheses it has been proposed by Drennan et al. (1993) that the sucrose and trehalose content of the leaves account for membrane stabilisation during the desiccated states. The refill after desiccation is facilitated by a unique lipid lining of the xylem (Wagner et al., 2000). Within ephemeral rock pools of granitic inselbergs, the poikilohydric aquatic plant *Chamaegigas intrepidus* (Scrophulariaceae) forms large mats at the water surface during the rainy season, while the rhizome survives desiccation during the dry season (Heilmeier and Hartung, 2011).

**3.4.4.1. Vegetation unit 15: *C. capitata*–*C. saxicola* rocky shrublands.** On rocky ground or shallow soils above rock, the *C. capitata*–*C. saxicola* unit is found. This unit inhabits a great richness in species and growth forms including many endemics and stem-succulent *Commiphora* species.

Due to its preference for rocky soils, this unit does not occur parallel to the major bioclimatic isolines, but rather reflects the presence of rocky surfaces along mountainous ranges such as the Chuos mountains. It is also found in erosion landscapes next to the major river systems, i.e. Kuiseb, Swakop, Khan and Omaruru. *C. glaucescens*, *C. saxicola*, *Commiphora tenuipetiolata*, *C. virgata*, *Cryptolepis decidua*, *Emilia marlothiana*, *E. desvauxii*, *E. glanduligera*



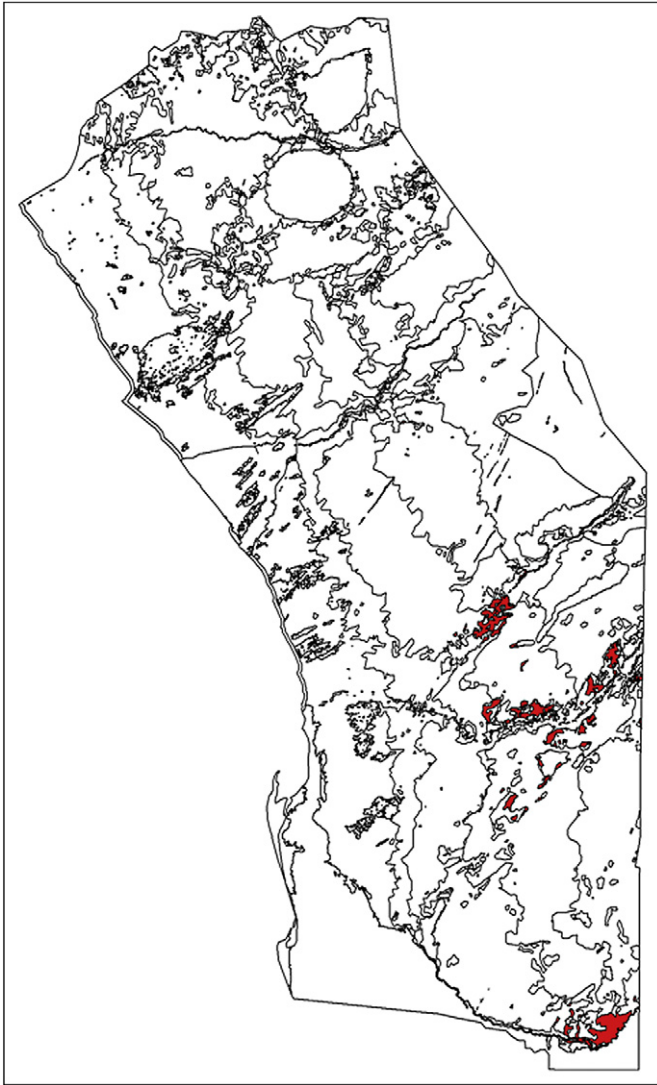


Fig. 16. Distribution of vegetation unit 17 *S. uniplumis* eastern grasslands.

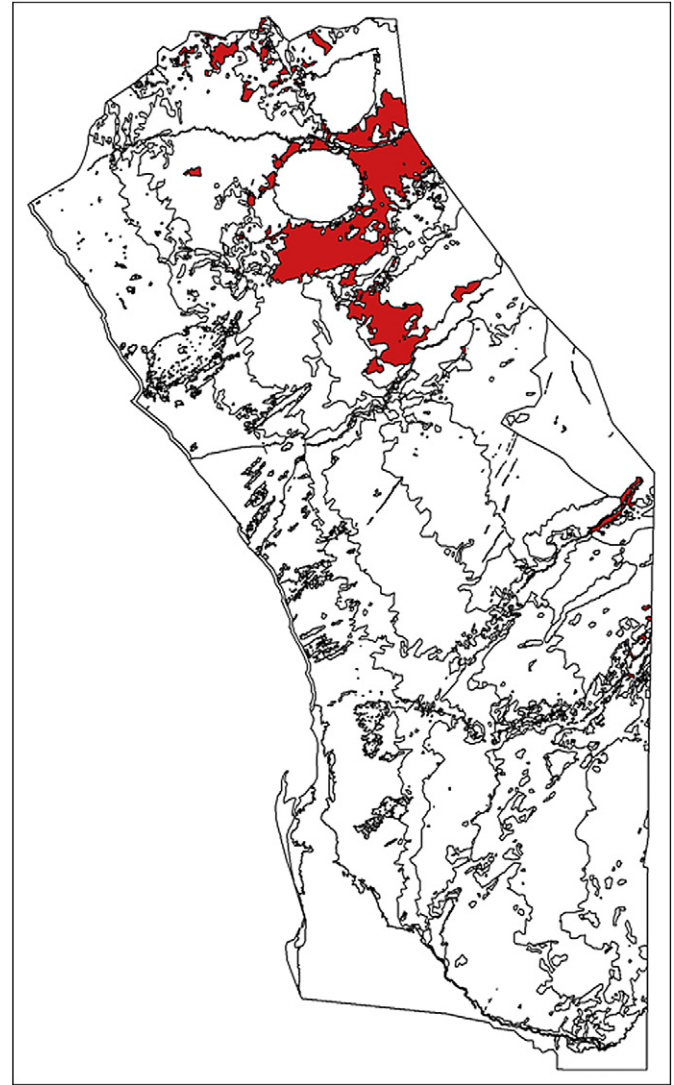


Fig. 17. Distribution of vegetation unit 20 *Stipagrostis hochstetteriana* eastern desert plains grasslands.

and *Euphorbia guerichiana* are important elements of this vegetation unit. Inland dolerite ridges were also included within this unit.

**Diagnostic environmental characteristics:** besides dolerite, the geology consists mainly of mica schist (class 44 in geology layer); considerable values for DAH and VRM. High MODIS-EVI values; partly highest rainfall values due to topography.

**Diagnostic species:** *C. capitata*, *C. glaucescens*, *C. saxicola*, *C. tenuipetiolata*, *C. virgata*, *C. decida*, *E. marlothiana*, *E. desvauxii*, *Enneapogon scaber*, *E. nindensis*, *E. glanduligera*, *E. guerichiana*, *S. hirtigluma* (Fig. 18).

**3.4.4.2. Vegetation unit 18: *E. damarana*–*C. capitata* stony and rocky desert succulent shrublands.** The large stem-succulent shrub *E. damarana* characterizes this vegetation unit. In the small growth form layer it partly overlaps with elements of the *C. capitata*–*C. saxicola* unit. The distribution area is not primarily controlled by climate as it forms longitudinal bands of SW-NE extension, i.e. at right angles to the climatic zonation. In the South, the two largest islands of this unit accompany two important river systems (Omaruru and Khan), suggesting a control by either topographical or geological drivers. However, in the Brandberg vicinity further north and in Damaraland, no such pattern is observed.

**Diagnostic environmental characteristics:** the distribution of this unit was partly modeled, partly digitized by hand on basis of Google Earth imagery. Geology is again of great importance: there are two dominant classes, mica schist (geological layer: 44) and meta-greywacke (geological layer: 72). The figures for both rainfall and temperature are generally high; the terrain is rather flat.

**Diagnostic species:** *B. foetida*, *E. damarana*, *P. variabile* (Fig. 19).

**3.4.4.3. Vegetation unit 21: *A. reficiens*–*C. mopane* eastern desert plains and hills savanna transition (thornbush savanna biome).** The Savanna biome is obviously not part of the central Namib Desert. Therefore, in this article the definition of the savanna unit remains comparatively rough. The savanna transition encompasses a range of tree species combinations, including at least two different plant communities: (i) *A. reficiens*-dominated sparse savanna, with or without *Acacia erubescens* and *Acacia senegal*; (ii) *C. mopane*-dominated savanna (only in the far Northeast of the project area).

With regard to habitat structure, the unit comprises very sparse to sparse to medium dense thornbush savanna formations only in zonal habitats. According to this definition, the western margin

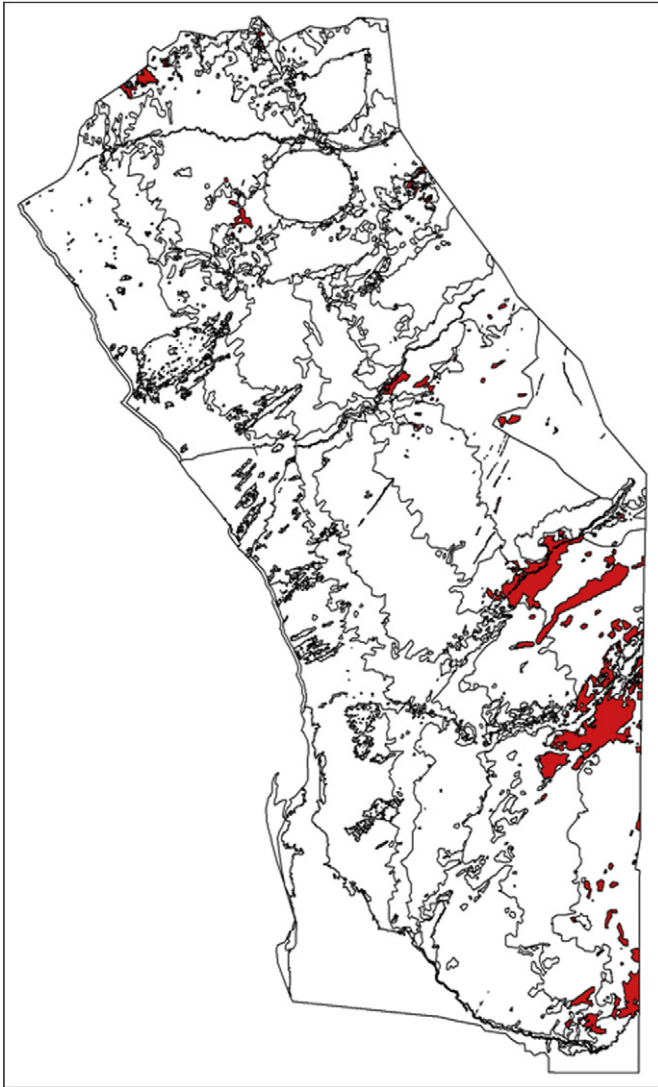


Fig. 18. Distribution of vegetation unit 15 *C. capitata*–*Commiphora saxicola* rocky shrublands.

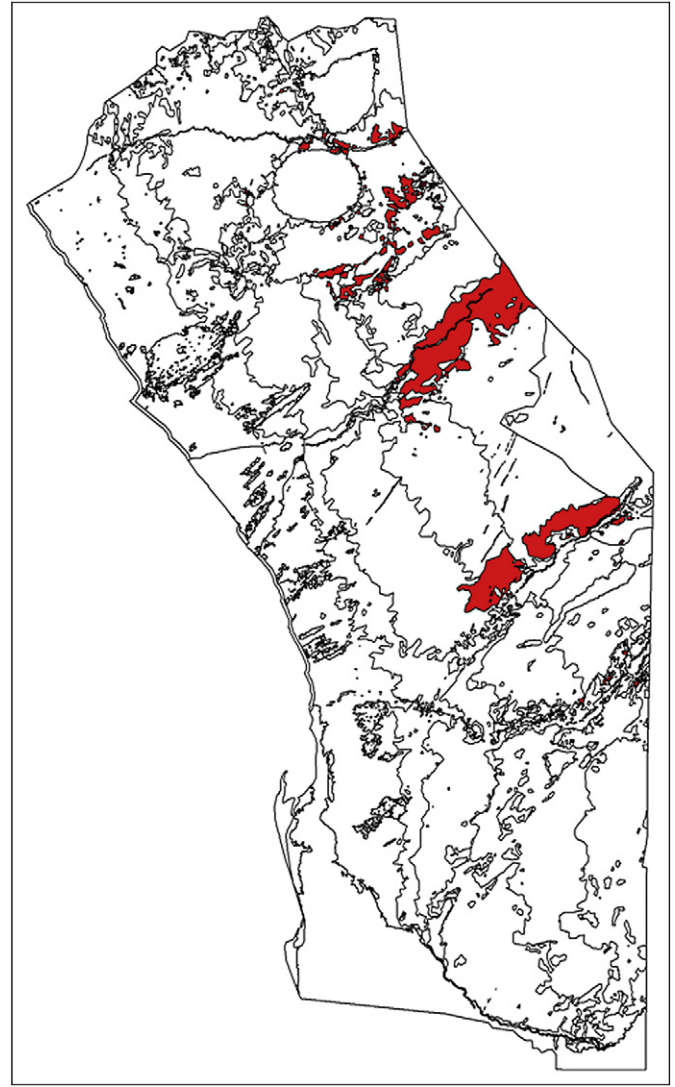


Fig. 19. Distribution of vegetation unit 18 *Euphorbia damarana*–*C. capitata* stony and rocky desert succulent shrublands.

of this unit is often characterized by the shift from “savanna” landscapes, where larger woody life forms (small trees and shrubs) cover the entire topography, to a “grassland” or “dwarf shrubland” landscape, where woody elements (small trees and shrubs) are limited to the lower-lying topographical elements like valleys, ephemeral rivers and other (even shallow) depressions, while the in-between plains and elevations are lacking such large woody life forms. The savanna unit also occurs and has its main distribution area outside the project area, i.e. the *Acacia reficiens* savanna east of the project area and the *Mopane* savanna northeast of the project area. There is a number of species endemic to Namibia that occur on the escarpment and also extend into this unit, e.g. *T. dimorphanthus*.

The *A. reficiens* savanna is vanishing at ca. 150 mm mean annual precipitation (MAP), while sparse *Mopane* savanna is even found between 100 and 150 mm MAP. However, in river beds, *A. reficiens* occurs in far more arid regions, even close to 50 mm MAP. It is obvious that the *A. reficiens* savanna is well developed where there is a flat transition between desert plains and the African Plateau, while the more southern parts of the Namib with a well-developed escarpment do not offer suitable habitats.

**Diagnostic environmental characteristics:** highest MODIS-EVI, rainfall and temperature values are recorded in this unit. A very broad range in minimum temperature values is found in this unit. The terrain is mainly flat on surficial deposits (Fig. 20).

**Diagnostic species:** *A. reficiens*, *B. foetida*, *C. mopane*, *G. alata*, *S. hochstetteriana*, *Terminalia prunioides*.

3.4.4.4. **Vegetation unit 23: Brandberg mountain vegetation (Nama Karoo and thornbush savanna biome).** The Brandberg has often been subdivided into three major vegetation belts, which are controlled by altitude. Wittneben (2003) sampled and analyzed an altitudinal transect at the Brandberg. He distinguished:

- Low altitude vegetation (750–1400 m a.s.l.): *Acacia montis-usti*–*Commiphora* spp. short sparse to open shrubland and bushland.
- Medium altitude (1400–2100 m a.s.l.): *Acacia hereroensis*–*Dombeya rotundifolia* short, open shrubland and low, closed thicket.
- Higher altitude vegetation (2100–2573 m a.s.l.): *Eriocephalus dinteri*–*Galenia africana* low shrubland; ephemeral herblands and grasslands; short closed shrubland.

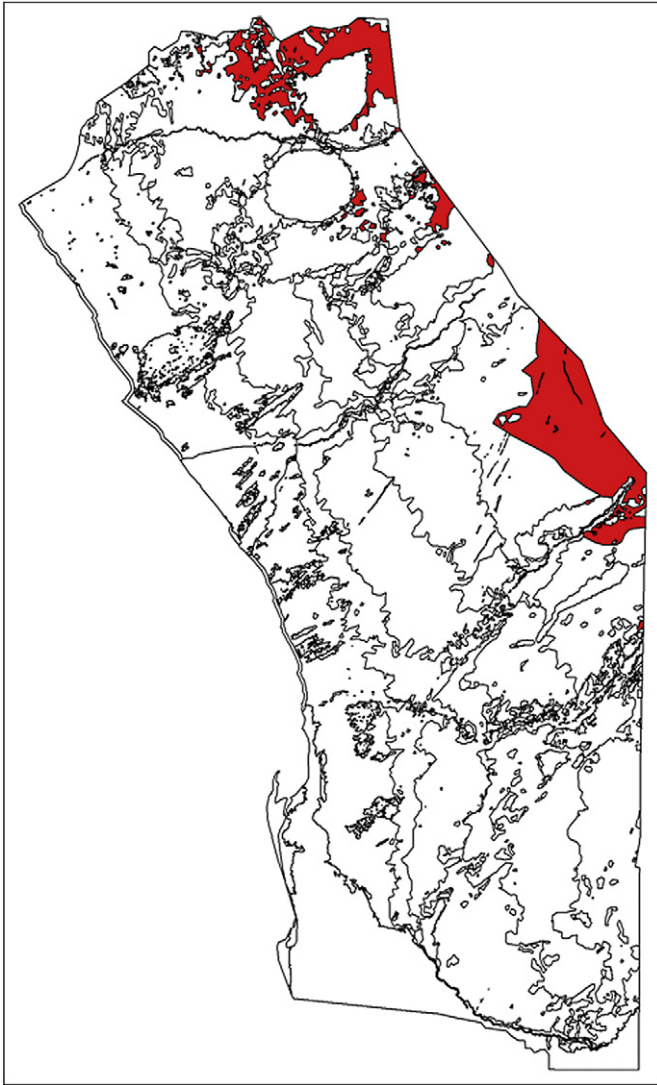


Fig. 20. Distribution of vegetation unit 21 *A. reficiens–Colophospermum mopane* eastern desert plains and hills savanna transition.

#### 4. Conclusions

The presented vegetation classification and vegetation map highlight that the flora of the central Namib Desert is composed of quite diverse units, related to two different floral kingdoms: the flora of the temperate Succulent Karoo biome belonging to the Greater Cape flora and the flora of the Nama Karoo belonging to the palaeotropical flora. These two major vegetation units make up 72% of the considered study area with the coastal zones including the Succulent Karoo elements and the unique lichen fields having 35.3% and the grasslands of the Nama Karoo having 41.6%. The spatial distribution of the 21 classified vegetation units is strongly controlled by climatic gradients, causing a series of vegetation belts, which run roughly parallel to the coastline. However, substrate is also a strong driver, shaping the distribution patterns within the climate-driven vegetation belts. Therefore, some vegetation units are not related to climatic gradients but mirror the spatial distribution of e.g. mobile dunes and rocky surface areas. Of the 806 plant species (belonging to 93 families), many show highly interesting features such as different forms of succulence and/or longevity developed to cope with the dynamic and harsh environment in

space and time. We identified 12% of the species as endemic to the Central Namib. This work provides a data and knowledge base on which future studies on the diversity and ecology of the species of the Central Namib can build. The database can also be used to inform conservation and management authorities by contributing important baseline information for regional assessment and conservation planning processes (see e.g. MET, 2012).

#### Contributors

NJ, BH and EE developed the initial mapping project. NJ and BH set up the methods, carried out the majority of field work and established the vegetation and floristic databases. JO built the GIS and carried out the modeling approach, integrated the majority of raster databases, tested the initial classifications and modeled the spatial distribution of the vegetation units. NJ provided the final classification, carried out quality control of the floristic record and ground truth validation of mapping results (several iteration steps). EE contributed to sampling of relevés, screened archives for historical photos and carried out a lot of long-term observation together with NJ and BH. CS carried out the classification, ground truth sampling, remote sensing interpretation and modeling of the lichen fields. The majority of text including description of units and review chapters was written by NJ. CS wrote the whole text regarding lichen fields. CS and JO wrote parts of the methodology. All authors contributed to the improvement of the manuscript.

#### Acknowledgements

NBRI and SANBI are thanked for allowing access and use of herbarium data for the vegetation analysis as circumscribed in the BIOTA project, funded by the German Federal Ministry of Education (gs1) and Research under promotion numbers 01 LC 0024, 01 LC 0024A and 01 LC 0624A2. We thank the Ministry of Environment of Namibia (MET) for granting permission for field work in protected and non-protected areas of the Central Namib. The authors acknowledge an earlier, different version of the vegetation map that was prepared as part of a landscape level assessment of key biodiversity vulnerability for the Central Namib (MET, 2012). Thanks to Ben Strohbach (NBRI) for allowing access and use of numerous additional relevés. We thank Ute Schmiedel and Judy Beaumont for supporting field data sampling and Judy Beaumont for improving the English text. Gerhard Mucbe is thanked for providing database extracts. We thank Nick Lancaster & Joh Henschel for their patience with regard to the submission of the manuscript.

#### Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jaridenv.2012.09.009>.

#### References

- Ad - Hoc Arbeitsgruppe Bodon, 1994. Bodenkundliche Kartieranleitung, fourth ed. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.
- Böhner, J., McCloy, K.R., Strobl, J. (Eds.), 2006. SAGA — Analysis and Modelling Applications. Verlag Erich Goltze GmbH, Göttingen.
- Boyer, D.C., Boyer, H.J., 1989. The status of alien invasive plants in the major rivers of the Namib Naukluft Park. Madoqua 16, 51–58.
- Burke, A., 1992. Aerial seed banks in the Central Namib: distribution of serotinous plants in relation to climate and habitat. J. Biogeogr. 19, 563–572.
- Burke, A., 1994a. Seed bank dynamics — longevity, viability and predation of seeds of serotinous plants in the central Namib Desert. J. Arid Environ. 28, 195–205.
- Burke, A., 1994b. Phenological niches of coexisting serotinous plants in the Namib Desert. J. Trop. Ecol. 10, 531–544.
- Burke, A., 1994c. Variability in life history parameters of four serotinous plants in the Namib Desert. Vegetation 114, 149–160.

- Burke, A., 1995. *Geigeria alata* in the Namib Desert: seed heteromorphism in an extremely arid environment. *J. Veg. Sci.* 6, 473–478.
- Burke, A., 2003. Floristic relationships between inselbergs and mountain habitats in the Central Namib. *Dinteria* 28, 19–38.
- Burke, A., 2008. The vegetation of the Spitzkoppe area – 2115CC. *Dinteria* 30, 93–131.
- Burke, A., Kyläkorpi, L., Rydgren, B., Schneeweiss, R., 2008. Testing a Scandinavian biodiversity assessment tool in an African desert environment. *Environ. Manage.* 42, 698–706.
- Cowlishaw, G., Davies, J.G., 1997. Flora of the pro-Namib Desert Swakop River catchment, Namibia: community classification and implications for desert vegetation sampling. *J. Arid Environ.* 36, 271–290.
- Curtis, B.A., 1990. Behaviour and ecophysiology of the Namib dune ant, *Camponotus detritus* (Hymenoptera: Formicidae). In: Seely, M.K. (Ed.), *Namib Ecology 25 Years of Namib Research*. Transvaal Museum Monograph, Pretoria, pp. 129–133.
- Curtis, B., Mannheimer, C., 2005. *Tree Atlas of Namibia*. National Botanical Research Institute, Windhoek.
- Dengler, J., Jansen, F., Glöckler, F., Peet, R.K., Cáceres, M.D., Chytrý, M., Ewald, J., Oldeland, J., Finckh, M., Mucina, L., Schaminée, J.H.J., Spencer, N., 2011. The global index of vegetation–plot databases (GIVD): a new resource for vegetation science. *J. Veg. Sci.* 22, 582–597.
- Drennan, P.M., Smith, M.T., Goldsworthy, D., van Staden, J., 1993. The occurrence of trehalose in the leaves of the desiccation-tolerant angiosperm *Myrothamnus flabellifolius* WELW. *J. Plant Physiol.* 142, 493–496.
- Ebner, M., Miranda, T., Roth-Nebelsick, A., 2011. Efficient fog harvesting by *Stipagrostis sabulicola* (Namib dune bushman grass). *J. Arid Environ.* 75, 524–531.
- Eckardt, F.D., Soderberg, K., Coop, L.J., Muller, A., Vickery, K.J., Grandin, R.D., Jack, C., Kapalanga, T.S., Henschel, J., The nature of moisture at Gobabeb, in the central Namib Desert. *J. Arid Environ.*, this issue, Available from: <http://dx.doi.org/10.1016/j.jaridenv.2012.01.011>.
- Eldridge, D.J., Rosentreter, R., 1999. Morphological groups: a framework for monitoring microphytic crusts in arid landscapes. *J. Arid Environ.* 41, 11–25.
- Giess, W., 1971. A preliminary vegetation map of South West Africa. *Dinteria* 4, 5–114.
- Giess, W., 1998. In: *A Preliminary Vegetation Map of South West Africa – Dinteria*, third ed., vol. 4. Namibia Scientific Society, Windhoek.
- Günster, A., 1993. Grass cover distribution in the Central Namib—a rapid method to assess regional and local rainfall patterns of arid regions? *J. Arid Environ.* 29, 107–114.
- Google Inc., 2011. Google Earth (Version 6.1.0.5001), Mountain View. Google Inc, California (Software).
- Hachfeld, B., 1996. *Vegetationsökologische Transektanalyse in der nördlichen zentralen Namib*. Diploma thesis, Universität Hamburg, Hamburg.
- Hachfeld, B., 2000. Rain, fog and species richness in the central Namib Desert in the exceptional rainy season of 1999/2000. *Dinteria* 26, 113–146.
- Hachfeld, B., Juergens, N., 2000. Climate patterns and their impact on the vegetation in a fog driven desert: the central Namib Desert in Namibia. *Phytocoenologia* 30, 567–589.
- Heilmeyer, H., Hartung, W., 2011. *Chamaegigas intrepidus* DINTER: an aquatic poikilohydric angiosperm that is perfectly adapted to its complex and extreme environmental conditions. In: Lüttge, U., Beck, E., Bartels, D. (Eds.), *Plant Desiccation Tolerance*. Ecological Studies. Springer, Berlin-Heidelberg, pp. 233–251.
- Hengl, T., Reuter, H.I. (Eds.), 2011. *Geomorphometry Concepts, Software, Applications*. Elsevier, Amsterdam.
- Henschel, J.R., Parr, T., 2010. Population changes of alien invasive plants in the Lower Kuiseb River. *Dinteria* 31, 5–17.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* 25, 1965–1978.
- Horning, N., Robinson, J.A., Sterling, E.J., Turner, W., Spector, S., 2010. *Remote Sensing for Ecology and Conservation: A Handbook of Techniques*. Oxford University Press Inc., New York.
- Huntley, B.J. (Ed.), 1985. *The Kuiseb Environment: The Development of a Monitoring Baseline*. Foundation for Research Development, Pretoria. Report no. 106.
- Jacobson, P.J., Jacobson, K.M., Seely, M.K., 1995. *Ephemeral Rivers and Their Catchments: Sustaining People and Development in Western Namibia*. Desert Research Foundation of Namibia, Windhoek.
- Juergens, N., 1991. A new approach to the Namib Region 1. *Phytogeographic subdivision*. *Vegetation* 97, 21–38.
- Juergens, N., 1994. *Phytogeography of the Namib and adjacent arid regions*. Habilitation dissertation at the Institut für Allgemeine Botanik, Universität Hamburg, Hamburg.
- Juergens, N., Niebel-Lohmann, A., 1995. *Geobotanical observations on Lichen Fields of the Southern Namib Desert*. *Mitt. Inst. Allg. Bot. Hamburg* 25, 135–156.
- Juergens, N., 1996. Psammophilous plants and other adaptations to desert ecosystems with high incidence of sandstorms. *Feddes Repertorium* 107, 345–359.
- Juergens, N., Burke, A., Seely, M.K., Jacobson, K.M., 1997. Desert vegetation of southern Africa. In: Cowling, R.M., Richardson, D.M., Pierce, S.M. (Eds.), *Vegetation of Southern Africa*. Cambridge University Press, Cambridge, pp. 189–214.
- Juergens, N., 2006. Recent change of flora and vegetation in Namibia – a brief review of dynamics, drivers and scientific approaches. *The Sixth Namibia Workshop Basel 2005*. In: Leser, H. (Ed.), *The Changing Culture and Nature of Namibia: Case Studies*. In Honour of Dr. h.c. Carl Schlettwein (1925–2005). Publishing House Basler Afrika Bibliographien, Basel – Windhoek, pp. 91–108.
- Juergens, N., Haarmeyer, D.H., Luther-Mosebach, J., Dengler, J., Finckh, M., Schmiedel, U., 2010. *Biodiversity in Southern Africa*. In: *Patterns at Local Scale – the BIOTA Observatories*, vol. 1. Klaus Hess Publishers, Göttingen.
- Loris, K., Schieferstein, B., 1992. *Ecological investigations on lichen fields of the Central Namib*. *Vegetation* 98, 113–128.
- Louw, G.N., Seely, M.K., 1980. Exploitation of fog water by a perennial Namib Dune Grass, *Stipagrostis sabulicola*. *S. Afr. J. Sci.* 76, 38–39.
- MET, 2012. *Landscape Level Assessment of Key Biodiversity Vulnerability and Land-use within the Uranium Province in the Central Namib*. Ministry of Environment and Tourism, Windhoek, Namibia.
- METI/NASA, 2009. *ASTER Global Digital Elevation Model by Ministry of Economy, Trade and Industry of Japan (METI) and the National Aeronautics and Space Administration (NASA)*. Available from: <http://www.asterweb.jpl.nasa.gov/gdem.asp> <http://www.gdem.aster.ersdac.or.jp/>.
- MDA Federal, 2004. *Landsat GeoCover ETM+ 2000 Edition Mosaics Tile S-33-00.ETM+earthsat-mrsid*, 1.0. USGS, Sioux Falls.
- Moore, J.P., Lindsey, G.G., Farrant, J.M., Brandt, W.F., 2006. An overview of the biology of the desiccation-tolerant resurrection plant *Myrothamnus flabellifolia*. *Ann. Bot. Lond.* 99, 211–217.
- Muche, G., Schmiedel, U., Juergens, N., 2012. *BIOTA Southern Africa biodiversity observatories vegetation database*. *Biodiversity Ecol.* 4, 111–123.
- Muche, G., Juergens, N., 2011. *BIOTA Collections – Software for Managing Botanical Collection Data*, Ver. 31.10.2011. Available from: [http://www.biota-africa.org/biotabase\\_ba.php?Page\\_ID=L900](http://www.biota-africa.org/biotabase_ba.php?Page_ID=L900).
- Naudé, Y., Van Rooyen, M.W., Rohwer, E.R., 2011. Evidence for a geochemical origin of the mysterious circles in the Pro-Namib Desert. *J. Arid Environ.* 75, 446–456.
- Neteler, M., Mitasova, H., 2008. *Open Source GIS: A GRASS GIS Approach*, third ed. Springer, New York.
- Picker, M.D., Ross-Gillespie, V., Vlieghe, K., Moll, E., 2012. Ants and the enigmatic Namibian fairy circles – cause and effect? *Ecol. Entomol.* 37, 33–42.
- Robinson, E.R., 1975. *Phytogeography of the Namib Desert of South Africa (Namibia) and its significance to discussions of the age and uniqueness of this desert*. *Palaeoecol. Afr.* 10, 67–74.
- Robinson, E.R., 1976. *Phytosociology of the Namib Desert Park, South West Africa*. M.Sc. thesis, University of Natal, Pietermaritzburg.
- Rogers, R.W., 1977. *Lichens of hot arid and semi-arid lands*. In: Seaward, M.R.D. (Ed.), *Lichen Ecology*. Academic Press, New York, pp. 211–252.
- Sappington, J.M., Longshore, K.M., Thompson, D.B., 2007. Quantifying landscape ruggedness for animal habitat analysis: a case study using bighorn sheep in the Mojave Desert. *J. Wildl. Manage.* 71, 1419–1426.
- Schenck, G., 1903. *Suedwest-Afrika, Tafel 25. Wüstenlandschaft zwischen dem Khanfluß und dem Khuos-Gebirge, nördlich vom Tsoakhoub (Swakop), mit Welwitschia mirabilis*. In: Karsten, G., Schenck, A. (Eds.), *Vegetationsbilder*, I. Reihe, 5. Heft. Gustav Fischer, Jena.
- Schieferstein, B., 1989. *Ökologische Untersuchungen an den Flechtenfeldern in der Namib-Nebelwüste*. Diploma thesis, Institute of Botany, Universität Hohenheim, Hohenheim.
- Schultz, C., 2006. *Remote sensing the distribution and spatiotemporal changes of major lichen communities in the central Namib Desert*. Ph.D. thesis, University of Kaiserslautern, Kaiserslautern, Germany.
- Schulze, E.-D., Ellis, R., Schulze, W., Trimborn, P., Ziegler, H., 1996. Diversity, metabolic types and <sup>13</sup>C carbon isotope ratios in the grass flora of Namibia in relation to growth form, precipitation and habitat conditions. *Oecologia* 106, 352–369.
- Seely, M.K., 1978. Standing crop as an index of precipitation in the Central Namib grassland. *Madoqua* 11, 61–68.
- Seely, M.K., de Vos, M.P., Louw, G.N., 1977. Fog imbibition, satellite fauna and unusual leaf structure in a Namib Desert dune plant *Trianthema hereroensis*. *S. Afr. J. Sci.* 73, 169–172.
- Seely, M.K., Buskirk, W.H., Hamilton III, W.J., Dixon, J.E.W., 1981. Lower Kuiseb River perennial vegetation survey. *J. S. W. Afr. Sci. Soc.* 35, 57–86.
- Strobbach, B.J., Juergens, N., 2010. Towards a user-friendly vegetation map of Namibia: ground truthing approach to vegetation mapping. In: Schmiedel, U., Juergens, N. (Eds.), *Biodiversity in Southern Africa. Patterns and Processes at Regional Scale*, vol. 2. Klaus Hess Publishers, Göttingen, pp. 45–56.
- Theron, G.K., van Rooyen, N., van Rooyen, M.W., 1980. Vegetation of the lower Kuiseb River. *Madoqua* 11, 327–345.
- Tichý, L., 2002. *JUICE*, software for vegetation classification. *J. Veg. Sci.* 13, 451–453.
- Tichý, L., Chytrý, M., Hájek, M., Talbot, S.S., Botta-Dukát, Z., 2010. Optimclass: using species-to-cluster fidelity to determine the optimal partition in classification of ecological communities. *J. Veg. Sci.* 21, 287–299.
- Van Rooyen, M.W., Theron, G.K., van Rooyen, N., Jankowitz, W.J., Matthews, W.S., 2004. Mysterious circles in the Namib Desert: review of hypotheses on their origin. *J. Arid Environ.* 57, 467–485.
- Vogel, J.C., Seely, M.K., 1977. Occurrence of C-4 plants in the Central Namib. *Madoqua* 10, 75–78.
- Von Willert, D.J., Eller, B.M., Werger, M.J.A., Brinckmann, E., Ihlenfeldt, H.-D., 1991. *Life Strategies of Succulents in Deserts*. Cambridge University Press, Cambridge – New York.
- Walter, H., 1936. *Die ökologischen Verhältnisse in der Namib-Nebelwüste (Südwestafrika) unter Auswertung der Aufzeichnungen des Dr. G. Boss (Swakopmund)*. *Jb. Wiss. Bot.* 84, 58–222.
- Wagner, H.-J., Schneider, H., Mimiertz, S., Wistuba, N., Rokitta, M., Krohne, G., Haase, A., Zimmermann, U., 2000. Xylem conduits of a resurrection plant contain a unique lipid lining and refill following a distinct pattern after desiccation. *New Phytol.* 148, 239–255.

- Ward, J.D., Seely, M.K., Lancaster, N., 1983. On the antiquity of the Namib. *S. Afr. J. Sci.* 79, 175–183.
- Werger, M.J.A., 1978. Biogeographical division of Southern Africa. In: Werger, M.J.A. (Ed.), *Biogeography and Ecology of Southern Africa*. W. Junk, The Hague, pp. 147–170.
- 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, South West Africa. *Madoqua* 14, 369–373.
- Wessels, D.C.J., 1989. Lichens of the Namib Desert, South West Africa/Namibia. *Dinteria* 20, 3–22.
- White, F., 1983. The Vegetation of Africa. In: UNESCO/AETFAT/UNSO Vegetation Map of Africa. UNESCO, Paris.
- Wittneben, M., 2003. Vegetation of the Brandberg Mountain, Namibia. M.Sc. thesis, University of Bremen, Bremen, Germany.
- Zhang, J., Kirby, R.P., 1999. Alternative criteria for defining fuzzy boundaries based on fuzzy classification of aerial photographs and satellite Images. *Photogramm. Eng. Rem. Sens.* 62, 1379–1387.

### Further reading

- Muche, G., Jürgens, N., Finckh, M., Schmiedel, U., 2011. BIOTABase – Software for Monitoring of Biodiversity and Environmental Data, Ver.16.04.1012. Available from: [http://www.biota-africa.org/biotabase\\_ba.php?Page\\_ID=L900](http://www.biota-africa.org/biotabase_ba.php?Page_ID=L900).