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Vol. 2

**Patterns and Processes
at Regional Scale**

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Biological soil crusts along the BIOTA Southern Africa transects

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Summary: Biological soil crusts (BSCs) were reported from six out of seven biomes along the BIOTA Southern Africa transects. Seven morphological BSC types were distinguished: three cyanobacteria-dominated crusts (types 1 and 2), one with additional cyanolichens (type 3), one type with chlorolichens (4), and one with bryophytes—either liverworts (type 5a) or mosses (type 5b). The hypolithic crust type (6) was restricted to quartz gravel pavements, and another one comprised the unique lichen fields of the Namib Desert (type 7). In total, at least 120 different species with 58 cyanobacteria, 29 green algae, one heterokont algae, 12 cyanolichens, 14 chlorolichens, two genera of liverworts, and three genera of mosses were found, placing these BSCs among the most diverse worldwide. They contribute considerably to the biodiversity of the arid and semi-arid regions of south-western Africa. The taxonomic diversity of cyanobacteria was higher in the winter rainfall zone than in the summer rainfall zone (54 versus 32 species). Soil photosynthetic biomass, carbon content and the number of BSCs revealed the same significant distribution patterns. Rainfall frequency and duration of dry periods rather than the precipitation amount seem to be the main factors influencing BSC growth and succession. This article is mostly based on the publication of Büdel et al. (2009).

Introduction

Biological soil crusts (BSCs) are an integral component of dry lands on all continents. They are an assemblage of microorganisms including cyanobacteria, algae, microfungi, lichens, liverworts and mosses in different proportions, which stabilise the upper few millimetres of the soil (Belnap et al. 2001). Their significant role within terrestrial ecosystems has only been recognised since the mid 20th century (Halperin et al. 1976, Komáromy 1976, Rogers et al. 1966, Shields et al. 1957, Skarpe & Henriksson 1987).

Within the sub-Saharan region, the southern and south-western parts of the African continent seem to be centres of BSC development (Ullmann & Büdel 2001). Vogel (1955) was one of the first to describe cyanobacterial and algal crusts underneath quartz gravels (= hypolithic) of the desert pavement, a community

that was later named the “hypolithon” (Schlesinger et al. 2003). Cyanobacterial soil crusts have been reported from the Kalahari region in South Africa, where they cover 11 to 95% of the Kalahari ground surface (Thomas & Dougill 2006, 2007).

In this investigation, we tested the following hypotheses: (1) the presence of BSCs on the soils of arid and semi-arid biomes is the rule and not the exception; (2) BSCs contribute considerably to the biodiversity of these biomes and are the primary colonisers of bare soils after disturbances of either natural or artificial disturbances; (3) BSC biomass (as chlorophyll content) rises with increasing species diversity; (4) the duration of drought periods and the frequency of rainfall events are the driving factors for the presence and development of BSCs and their diversity rather than the total amount of annual rainfall; (5) the struc-

tural composition of soils influences the presence and diversity of BSCs.

Material and methods

For a detailed description of material and methods see Büdel et al. (2009).

Results

Classification of biological soil crusts

Seven main BSC types were distinguished in the 28 Observatories along the BIOTA transects (Figs. 1, 4–9). (1) Early successional crusts were brittle, less than three millimetres thick, and could be recognised with the naked eye by a slight and patchy discoloration of the soil surface (Fig. 4). They were composed of filamentous cyanobacteria, e.g. *Microcoleus* and *Lepidoglyngbya*. (2) The intermediate succession crust was a well established cyanobacterial crust, up to 3.9 mm thick, and included additional cyanobacterial species. The soil was not only stabilised by the presence of this crust type but also had a predominantly dark discoloration on its surface. When undisturbed, this type could develop into the late succession crust, which included (3) cyanobacterial lichens (Fig. 5), (4) chlorolichens or both (Fig. 6). Where precipitation events like rain or dewfall were frequent enough, (5a) liverworts (Fig. 7) or (5b) mosses developed. Later on, type 5a and 5b may have occurred without cyanobacteria and lichens. (6) Hypolithic crusts were restricted to the occurrence of translucent quartz gravel on the ground (Fig. 8). (7) Due to their structure and high green algal lichen diversity, the crusts of the Namib Desert were considered as a unique BSC type (Fig. 9).

The effectiveness of the presented classification scheme was reflected by significant

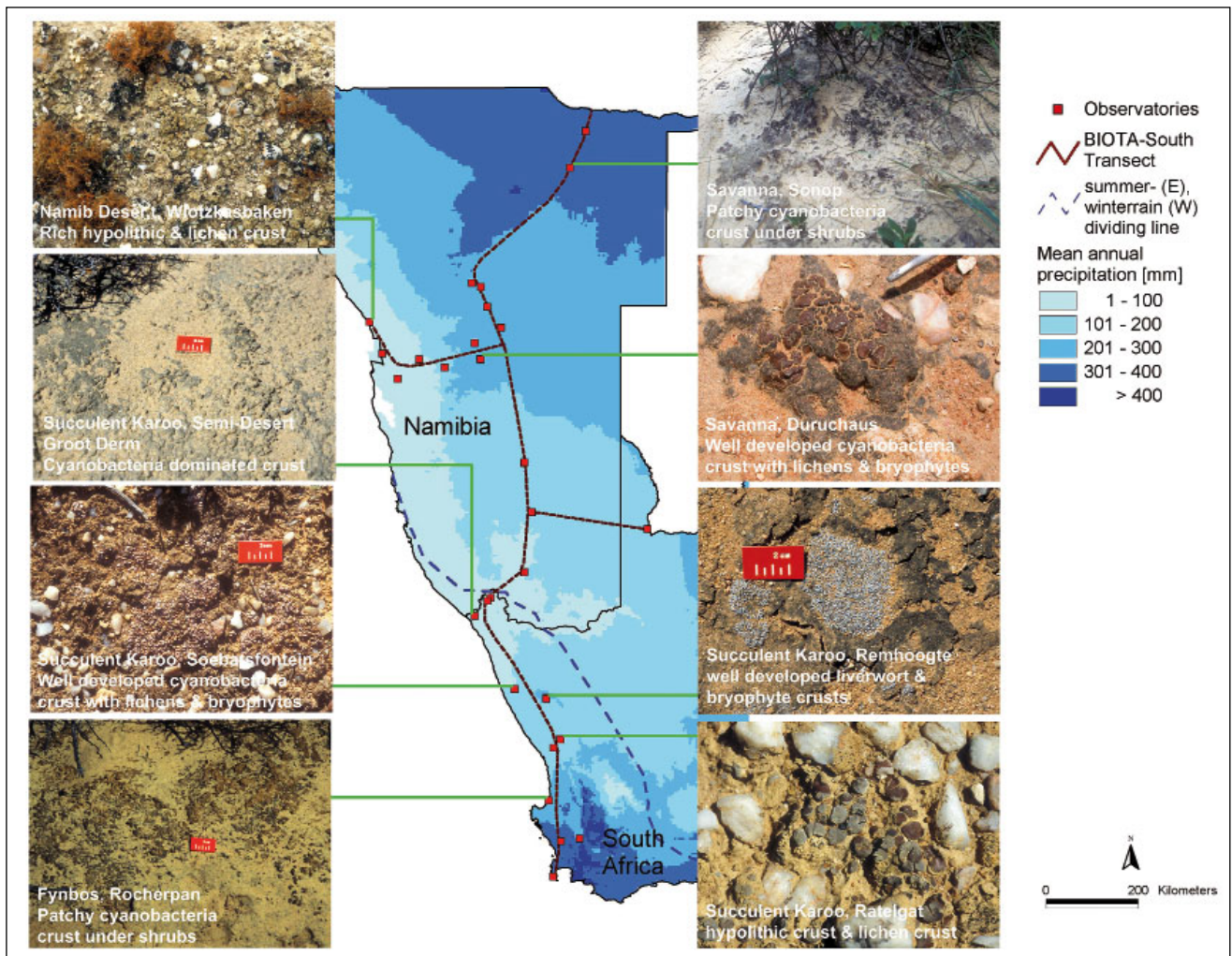


Fig. 1: Crust types occurring at the Observatories along the transects.

differences of several parameters between crust types. Crust thickness of the three BSC types increased with crust development from the early (type 1; 2.7 ± 0.224 mm, $N = 4$) to the intermediate (type 2; 3.4 ± 0.99 mm, $N = 13$) and the late (type 3; 4.4 ± 0.89 mm, $N = 13$) successional stages. In a one-way ANOVA, crust thickness was shown to be significantly different between the groups ($p = 0.002$, $N = 3$), and posterior F statistics revealed significant differences between both types 1 and 3 ($p = 0.002$) and types 2 and 3 ($p = 0.006$).

Similarly, the biomass values increased with higher successional stage. Chlorophyll_a and chlorophyll_{a+b} both revealed a considerable increase from an early succession crust stage (type 1; 31.8 ± 14.97 mg chl_a/m², 49.3 ± 28.25 mg chl_{a+b}/m²) to the intermediate (type 2; 67.9 ± 46.33 mg chl_a/m², 112.5 ± 80.89 mg chl_{a+b}/m²) and the late

(type 3; 86.3 ± 31.62 mg chl_a/m², 135.8 ± 46.5 mg chl_{a+b}/m²) successional stages. For both factors, significant differences between the groups were shown using a one-way ANOVA (chl_a, $p = 0.005$, chl_{a+b}, $p = 0.004$), and posterior F statistics revealed significant differences between crusts of types 1 and 2 (chl_a, $p = 0.026$, chl_{a+b}, $p = 0.014$) as well as types 1 and 3 (chl_a, $p = 0.001$, chl_{a+b}, $p = 0.001$). Besides that, we found that high chl_a values were also associated with a high number of different BSC types (Pearson correlation coefficient 0.64). There was no correlation between BSC characteristics and carbon or nitrogen content of the soil.

Distribution patterns of BSC types and abiotic factors along the transects

BSCs of various types were found in all biomes except for the Fynbos biome.

The highest degree of coverage (up to 70%) was observed in the Namib Desert with crust types 6 and 7, a value close to those found by other authors of up to 87% of the soil surface (Lalley et al. 2006, Schieferstein & Loris 1992). This was followed by the Savanna ecosystems (up to 60%) with mainly crust types 1–4 and rarely 5, and the Succulent Karoo (up to 35%), where all types of crusts were present, except the lichen field type 7. In the Nama Karoo, mostly the early successional stages of BSCs (type 1) were observed, with a low coverage of less than 6%. Hypolithic crusts (type 6) were also scattered over the area.

At the Zambesian dry forest Observatories, mainly type 1 and rarely type 2 BSCs with low-coverage values for both (< 1%) were encountered and their presence was restricted to recently burned areas. The Woodland Savanna Biome

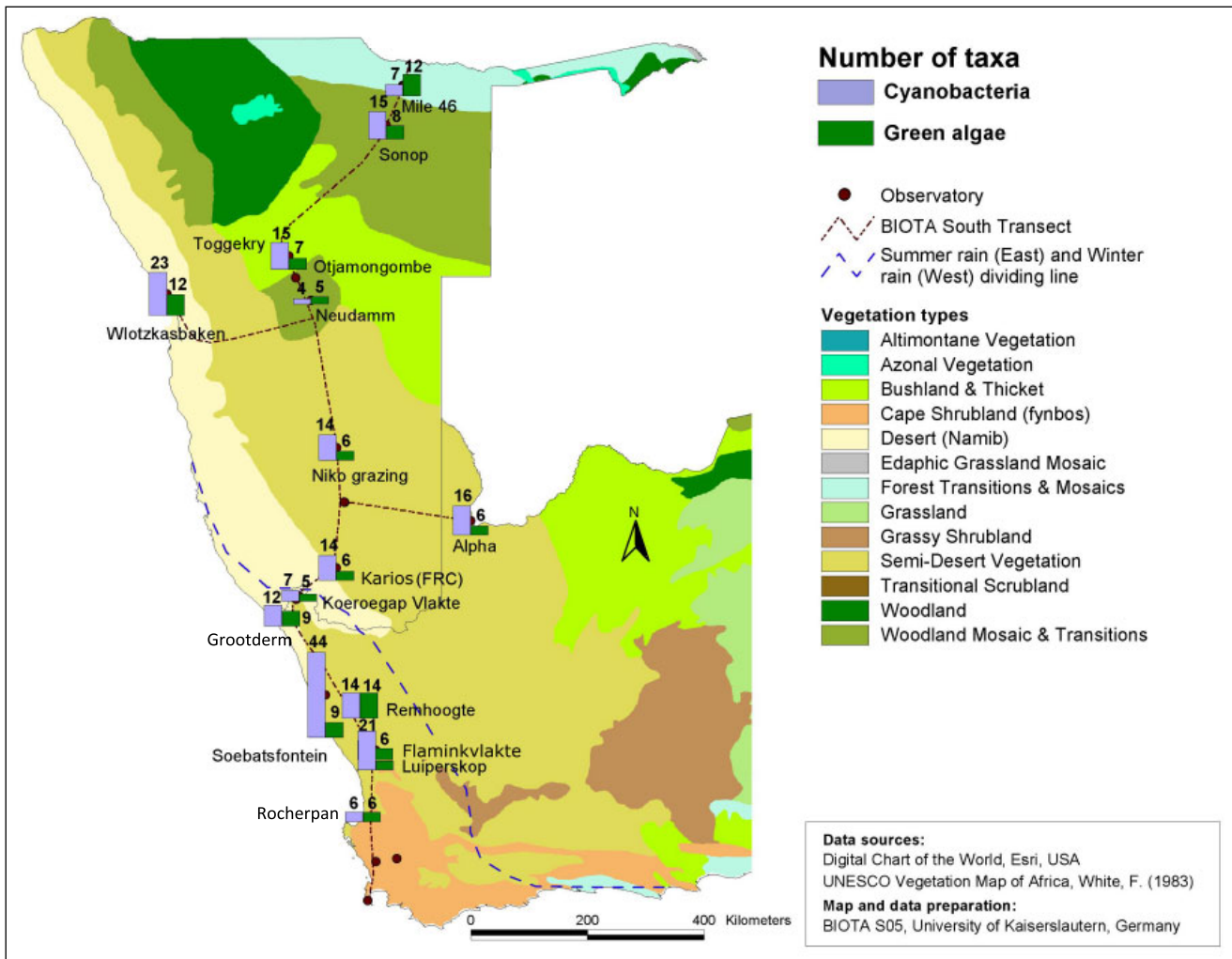


Fig. 2: Number of algal taxa at the different Observatories along the transects.

exhibited BSC types 1–4 and 6, which grew underneath exposed, scattered quartz rocks, with type 2 and 4 BSCs being the most common. BSC coverage was between 20–60%. Bryophyte crusts were extremely rare in this biome. BSCs of the types 1–2 (very rarely type 4 and 5) often occurred underneath the canopy of shrubs. In the Namib Desert, the especially diverse BSC type 7 occurred within the spectacular lichen fields, but type 6 BSCs were also common within the quartz gravel pavements. In the fog zone of the desert, type 7 crusts covered up to 70% of the total area investigated revealing chlorophyll values of $156.2 \pm 64.68 \text{ mg chl}_a/\text{m}^2$ and $230.5 \pm 98.33 \text{ mg chl}_{a+b}/\text{m}^2$ ($N = 9$). Although present in the Kalahari Highveld, type 1 BSC occurrence was very scattered, patchy and of extremely low biomass. BSCs in the Nama Karoo biome mainly belonged to type 1, but

type 6 crusts were also common where a quartz gravel pavement was present. Here, BSCs were found only at one BIOTA Observatory (i.e. Niko North, Observatory S08, coverage up to 5%).

The Succulent Karoo Biome was commonly inhabited by six types of BSCs, with the large quartz fields of the Knersvlakte being characterised by a particularly high coverage and species diversity of type 6 BSCs (up to 25% of the soil surface). These hypolithic crusts of the Knersvlakte comprised mean chlorophyll values of $74.5 \pm 37.11 \text{ mg chl}_a/\text{m}^2$ and $107.3 \pm 47.13 \text{ mg chl}_{a+b}/\text{m}^2$ ($N = 8$). Biological soil crusts with cyanolichens and/or chlorolichens as well as liverworts and/or mosses (type 5a and b) were well developed within this Biome. The Observatory in the Fynbos biome showed some growth of pro- and eukaryotic algae in the soil, but despite intensive search-

ing, no crust formations were detected on the soil surface. In the savanna and semi-desert biomes, early succession crust types were often observed developing in the dripping zone of shrubs.

The soils along the transects were generally nitrogen depleted and exhibited values between 0.1 g/kg (Zambesian dry forest) and 0.6 g/kg (dry Savanna, Succulent Karoo) total nitrogen per dry matter. This resulted in high C:N values (e.g. above 100 in the Nama Karoo), indicating the limiting role of N in the soil. A positive correlation between the number of BSC types and the proportion of silt and clay in the soil (Pearson correlation coefficient 0.52, $p = 0.04$) was found.

Diversity of species

BSCs were present in all biomes except the Fynbos and at most Observatories along the transects (Fig. 2). In total, we

recorded 58 species of cyanobacteria, 29 green algae, one heterokontophyte, 12 cyanolichens and 14 chlorolichens. Many cyanobacteria taxa were only found at one or two Observatories. The majority of cyanobacteria occurred in Observatories of both major rainfall regimes. For a list of species see the detailed Observatory descriptions in Part II of this book. The number of cyanobacteria species was considerably higher in the winter rainfall zone (54 species) than in the summer rainfall zone (32 species). In the winter rainfall zone, the cyanobacteria reached their highest diversity in the Succulent Karoo (49 species), whereas in the summer rainfall zone the highest species diversity was recorded in the Thornbush Savanna (22 species).

The diversity of eukaryotic algae was similar in both rainfall regime types with 23 species in the winter rainfall zone and 22 in the summer rainfall zone (Fig. 2). The highest species numbers were found in the Succulent Karoo Observatories (19 species, winter rainfall) and the Observatories of the dry savanna (16 species, summer rainfall). Species numbers in the other biomes were all below ten. Generally, the species-rich biotopes were located in the northern parts of the transect and along the coast. Among the eukaryotic algae, 15 species were found at least three times. Most of them were observed in both winter and summer rainfall zones, with only four occurring exclusively in the summer rainfall zone and none exclusively in the winter rainfall zone.

The initial stages of soil crusts were always composed exclusively of cyanobacteria. Eukaryotic algae were common soil organisms and were also present in the BSCs reported here. However, they were not observed to form BSCs themselves in the biomes along the transect. While the cyanobacterial diversity correlated significantly with the mean chl_a and chl_{a+b} content (Pearson correlation coefficients of 0.58 and 0.51), this was not the case for green algae. Of the 26 recovered lichen species 12 were cyano- and 14 chlorolichens.

Relevance of rainfall frequency and regime

Total precipitation was significantly higher in the summer rainfall zone compared

to the winter rainfall zone, while the duration of drought was significantly shorter in the winter rainfall zone. The mean chlorophyll content in the winter rainfall zone (67 mg chl_a/m², 102 mg chl_{a+b}/m²; $N = 29$) was significantly higher than in the summer rainfall zone (39 mg chl_a/m² and 68 mg chl_{a+b}/m²; $n = 27$). Maximum values in the winter rainfall zone were well above 100 mg chl_a/m², and 200 mg chl_{a+b}/m². Dry-matter-related biomass in terms of carbon content was also significantly higher in the winter rainfall zone (1.9 versus 1.1, $U_{21, 21} = 135$, $p = 0.031$) and the number of BSC types per Observatory was also significantly higher (1.8 versus 1.1; $U_{27, 29} = 261.5$, $p = 0.028$).

Diversity, rainfall regime/frequency, and soil

Relating BSC characteristics to site characteristics along the transects (Fig. 3), we found a positive correlation between the number of BSC types as well as chl_a content with winter rainfall frequency (Pearson correlation coefficient: 0.51, $p = 0.036$, and 0.6, $p = 0.01$), and a negative correlation between the number of BSC types with summer rainfall frequency (Pearson correlation coefficient: -0.54 , $p = 0.024$). The winter rainfall zone was characterised by a significantly shorter annual dry period (89 days versus 153 days in the summer rainfall zone, $U_{8, 9} = 5.0$, $p = 0.003$) with a more even distribution of rainfall events over the year (64 days in summer versus 80 days with rain in the winter rain zone, not significant) and a higher winter rainfall frequency (number of rainy days during the winter period from April to September).

Discussion

Species richness

The cyanobacterial diversity recorded in this study is probably the highest reported so far for BSCs occurring in arid and semi-arid regions around the world, with a total of 58 species of which 49 occurred in the Succulent Karoo and 24 in the Namib Desert.

Many of the 31 eukaryotic algal species detected in soil crusts along the Namibia–South Africa transect have already been

reported from BSCs of other continents. As already described for cyanobacteria, the green algal diversity was highest in the BSCs of the Savanna (20) and the Succulent Karoo (29) biomes. No other BSC reported so far has shown such a high species richness in eukaryotic algae. The pro- and eukaryotic algal α -diversity of different BSC types seems to be correlated with a higher fine-grain fraction in the soil. For lichens and bryophytes, we have not yet been able to show a clear distribution pattern with regard to macroclimatic factors. With regard to total species richness of lichens and mosses, our random sampling showed its weaknesses. Since most lichens (26 species in 14 genera) and also many bryophytes have patchy distributions, we in all likelihood failed to collect the complete diversity. For comparison, in BSCs of the Columbia Basin (USA) as many as 144 lichen species were reported (McCune & Rosentreter 2007). Nevertheless, it appears that their occurrence in BSCs depends on longer periods between disturbances and more frequent rainfall events with shorter drought periods in between (Belnap & Lange 2001).

Our results reveal a significantly higher cyanobacterial species richness of BSCs in winter rainfall areas (summer versus winter, 32:54 species). This finding partly confirms the third hypothesis in that BSCs contribute to the biodiversity of their biomes. An increasing diversity of cyanobacteria was found with an increasing diversity of BSC types, which partly confirms our third and fifth hypotheses. An increase in cyanobacterial species numbers was found to be correlated with a biomass increase, partly confirming our fourth hypothesis.

Biological soil crust presence, diversity

The successional progress starting from BSC type 1 containing only cyanobacteria and ending with types 3, 4, and/or 5 illustrates the importance of cyanobacterial sheaths for crust development and soil consolidation, whereas lichens and bryophytes contribute mainly to the high chlorophyll (biomass) values of BSCs. In the *Acacia mellifera* thorny shrubland of the Kalahari Desert, Botswana, an ex-

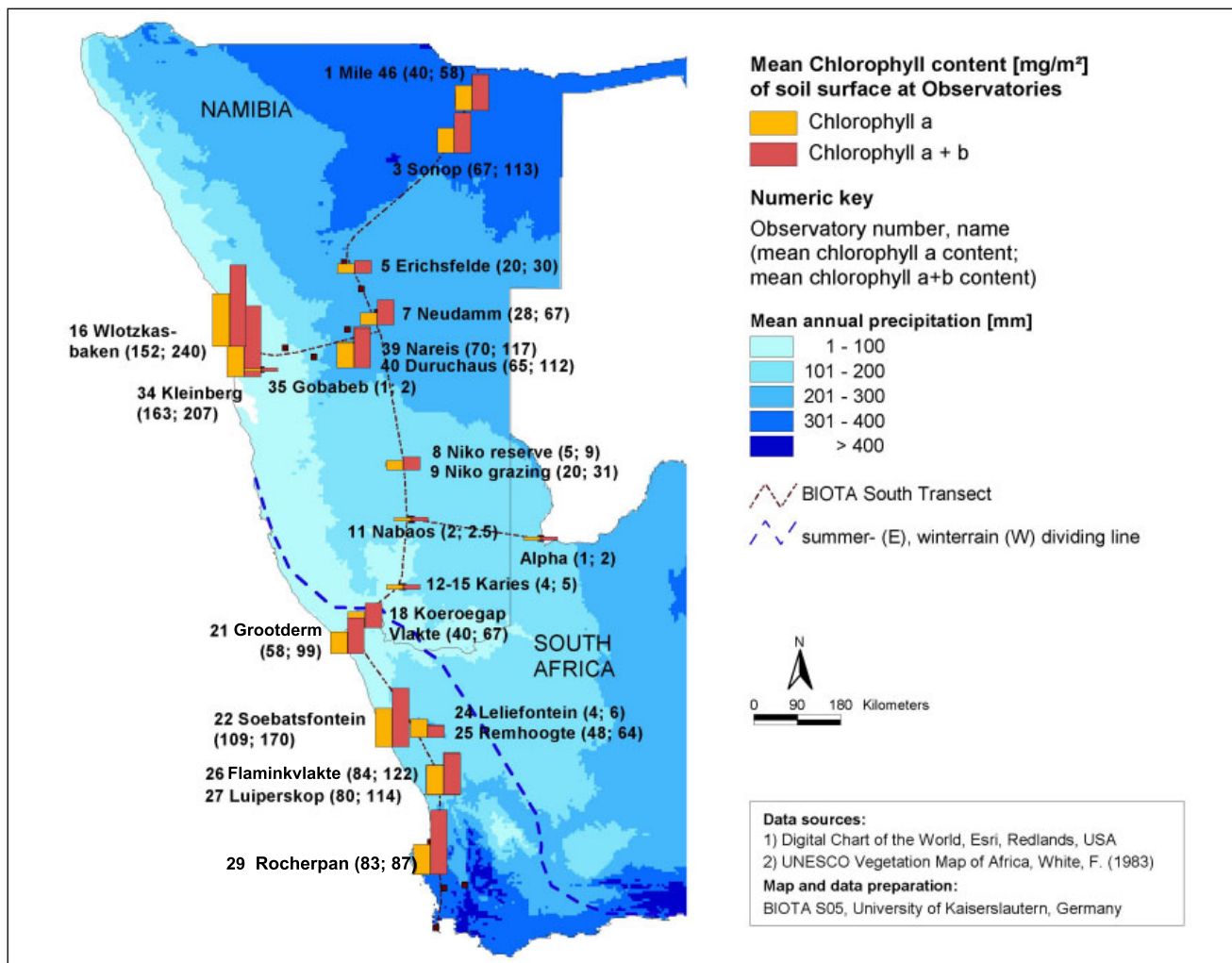


Fig. 3: Chlorophyll content of BSCs at the different Observatories along the transects.

tensive cyanobacterial crust was found, 3–4 mm thick and comparable to type 1 and 2 of our study, that covered between 11 and 95% of the bare soils (Dougill & Thomas 2004, Thomas et al. 2002, Thomas & Dougill 2006, 2007).

The very specialised hypolithon (type 6) is not only composed of a number of different cyanobacteria and green algae, but lichens and bryophytes are also reported from their protecting and moisture gathering habitat (Büdel & Schultz 2003, Vogel 1955, Werger & During 1989). While the hypolithic crust (type 6) also occurs in other arid and semi-arid parts of the world (Cockell & Stokes 2004, Schlesinger et al. 2003), the lichen fields (type 7) are unique to the Namib Desert with their unrivalled but not yet fully known lichen diversity and their wide extent (Loris et al. 2009, Articles III.3.6, III.3.7). They differ considerably

from the other BSC types along the BIOTA Southern Africa transects. In addition to terricolous crustose lichens involved in crust formation, foliose and fruticose lichens occurred. Chlorophyll values of the Namib Desert crusts represent the highest ones measured along the transect, reaching mean values of 156.2 mg chl_a/m² and 230.5 mg chl_{a+b}/m². In a *Lecidella crystallina*-dominated crust system, Lange et al. (1994) determined as much as 508 mg chl_{a+b}/m², a chlorophyll content amongst the highest values known for BSCs worldwide (Lange 2001). They have two unique features: the absence of cyanolichens (O.L. Lange, personal communication), and the apparent limitation of cyanobacteria to hypolithic habitats.

From the above we can confirm hypothesis 1, that BSCs are a regular and common part of the vegetation in southwestern Africa, with the exception of the

Fynbos Biome. The recording of seven different BSC types confirms our second hypothesis. The lack of BSCs in the Fynbos Biome is puzzling, especially since free-living soil algae are known to be present. Until now, we have been unable to explain this absence, but it is interesting to note that within the Fynbos Biome the soil pH is always well below pH 4 (Petersen 2008). While BSC type 1 is always an early successional type, crusts of type 2 can either be intermediate successional stages, eventually developing into types 3–4, or are the final stage (“climax”) reached under the given circumstances. Biological soil crusts of types 3 and 4 are late successional stages and may develop into type 5, but can also be climax stages. Biological soil crusts of types 6 and 7 always represent “climax” crusts.



Fig. 4: Early successional crust composed of cyanobacteria, type 1, Otjiamongombe, savanna.



Fig. 5: Intermediate to later successional crust with cyanobacteria and first cyanolichens (*Heppia* sp., *Collema* sp.), type 3, Duruchaus, savanna.



Fig. 6: Late successional/climax crust with additional chlorolichens (*Psora decipiens*), type 4, Soebatsfontein, dry savanna to semi-desert.

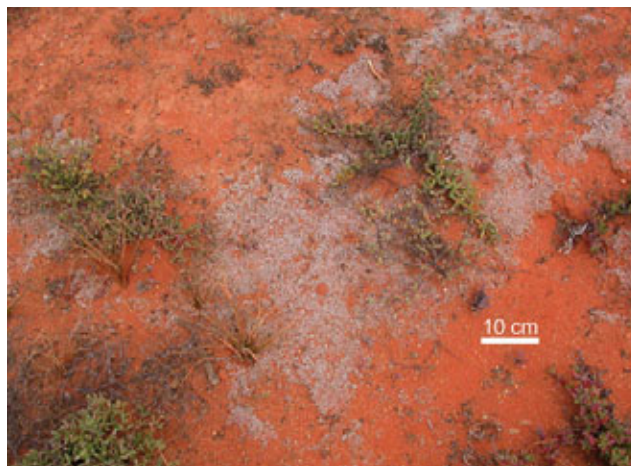


Fig. 7: Climax crust with the liverwort *Riccia* sp., type 5a, Soebatsfontein.



Fig. 8: Hypolithic crust with cyanobacteria, type 6, Karios near Fish River Canyon, Desert Biome.

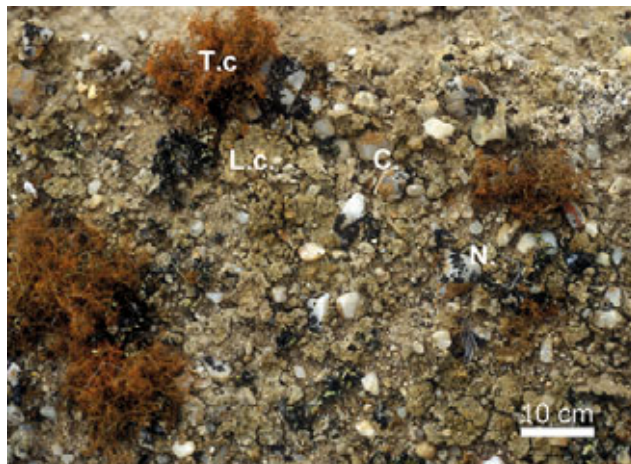


Fig. 9: Climax crust: the unique lichen fields of the Namib Desert (chlorolichens and a few cyanobacteria), type 7, Wlotzkasbaken, Desert Biome. L.c. = *Lecidella crystallina*, N. = *Neofuscellia* sp., T.c. = *Teloschistes capensis*, C. = *Caloplaca* sp.

Climatic and edaphic factors

Since BSC diversity and species richness, as well as biomass were correlated with a higher rainfall frequency and with shorter annual dry periods in the winter rainfall zone, it would appear that precipitation frequency rather than the total amount of annual precipitation is the discriminating factor for BSC growth and succession. However, it is necessary to point out, that a higher rainfall frequency will only enhance BSC development if rainfall events are substantial enough to allow the organisms to reach or exceed their photosynthetic net compensation points. If precipitation during rainfall events is too low or air temperatures are very high, this may lead to a carbon deficit, and frequent recurrence of such conditions may even cause the death of the organisms. These correlations corroborate our fourth hypothesis, suggesting that long drought periods slow down BSC succession, reduce biomass gain, and negatively affect organisms sensitive to drought periods, such as lichens and bryophytes. A positive correlation between the number of BSC types and the proportion of silt and clay in the soil (Pearson correlation coefficient 0.52, $p = 0.04$) might indicate that fine-grained soils are important for BSC development. It also appears that higher chl_a content is associated with fine-grained soils, thus confirming our fifth hypothesis.

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