Diversity change of soil-growing lichens along a climate gradient in Southern Africa

Luciana ZEDDA and Gerhard RAMBOLD

Lehrstuhl für Pflanzensystematik und Ökologie, Abt. Mykologie, Universitätsstraße 30, NW I, D-95445 Bayreuth, Germany

Abstract: The diversity of lichens forming biological soil crusts along a climate and vegetation gradient in Southern Africa has been investigated at 22 selected observatories, each of 1 km². A total of 59 taxa of soil-growing lichens are reported with some new records from the study area (*Collema texanum, Diploschistes* cf. *thelenelloides, Lecanora pseudistera, Peccania* aff. *fontequeriana, Placidium lacinulatum* and *Toninia* aff. *ruginosa*). Most of the recorded species are crustose. Foliose and fruticose lichens were found to be restricted to those observatories highly influenced by fog and with higher air humidity. The distribution of soilgrowing lichens is apparently not related to the quantity of precipitation, but is more dependent on the rain system, on fog events and air humidity (vicinity to the coast). Soil-growing lichens are in fact most frequent and abundant in regions with a winter rain system rather than in summer rain regions. Sandy soils are unfavourable substrates for lichen growth, being too unstable, and at some of the investigated observatories, the effect of man-made disturbance on lichen diversity were also observed. For these reasons, lichens appear to be good indicators of environmental changes in the study area.

Introduction

Biological soil crusts are composed of lichens, bryophytes, microalgae, microfungi and cyanobacteria which live within or immediately on top of the uppermost soil layers. In arid and semi-arid regions they are able to survive by utilizing small rain events, fog and dew as water sources where moisture deficit limits vascular plant cover. Desert habitats with fog and dew favour the occurrence of phycolichens, whereas cyanolichens are found in areas lacking dew, due to higher temperatures and less rainfall. Lichens, together with bryophytes, are usually found at advanced stages of succession of biological soil crust communities, on highly stable soils (gypsum and calcite) and under rather undisturbed conditions, and are therefore important indicators of the degree of human impact on the environment (BELNAP & LANGE 2001). Most studies on the monitoring of biological soil crusts concern Australia and North America where different investigation and monitoring methods have been applied (ROGERS & LANGE 1971, 1972; ROGERS 1972a, b; WEST 1990, BELNAP & LANGE 2001; BELNAP *et al.* 2001); no correlative studies exist for Southern Africa.

Hitherto, lichens of biological soil crust communities in Southern Africa were rather poorly investigated (ROGERS 1977). Most studies were focussed mainly on taxonomic questions, whereas floristic and vegetation studies were restricted to certain regions as the Namib desert (SCHIEFERSTEIN 1989; SCHIEFERSTEIN &

LORIS 1992; JÜRGENS & NIEBEL-LOHMANN 1991, 1995). A recent account on the state of lichenological activities in the Namib and Karoo regions of Southern Africa is given by ULLMANN & BÜDEL (2001).

In the context of the recently installed BIOTA Southern Africa project (http://www.biota-africa.de/1024/start.htm), a long-term survey of soil-growing lichens was initiated. The BIOTA project is an interdisciplinary research project analysing biodiversity and its change along a climatic and vegetation gradient from northern Namibia to the Cape Peninsula (Republic of South Africa). The main aim of the subproject on lichens is the assessment of lichen diversity along a north-south transect, analysing the spatial and temporal changes in biodiversity in relation to abiotic and biotic factors such as climate, pedodiversity and land use. It is also intended to elaborate the indicator value of terricolous lichen taxa and communities for the study area, to be used in a future long-term monitoring survey.

This work presents the first results on changes in diversity of soil-growing lichens that form biological soil crusts along this transect. The changes are analysed in relation to climate, especially to the mean annual precipitation, rain system and fog events, as well as to soil and land use systems.

The study area

The BIOTA South transect is located along a climate gradient from regions characterized by a summer rain system (in Namibia) to regions with a winter rain system (Northern Cape and Western Cape Provinces, RSA). The climate is dominated by anticyclonic circulation patterns together with the effects of the high escarpment rims of the plateau formed by the Drakensberg Mountains in the east and the Cape fold mountains in the south, as well as by the cold Benguela Current along the Atlantic coast (WERGER 1986). Mean annual precipitation varies from less than 50 mm to about 600 mm. The lowest mean annual precipitation is recorded along the coasts of the Namib Desert (< 50 mm), in Southern Namibia, in the Richtersveld area and in Namaqualand (100–150 mm/year). The highest precipitation is recorded in northern Namibia (about 550 mm/year) and in the Cape Peninsula (more than 600 mm/year). There is also a clear precipitation gradient from west to east over the entire area (WERGER 1986).

Fog is due to the effects of the Benguela Current and is carried by sea breeze from the sea towards the land where it creates a light and fine rain and dissipates slowly during the day (WALTER 1986). Fog is common and of great ecological importance along the coast as it greatly contributes to the available amount of moisture. At Swakopmund (Namib desert), for instance, there is an average of 121 foggy days per year with a maximum in wintertime. The precipitation from this fog equals about 130 mm of rainfall per year and may equal about 300 mm of rain over the most arid winter-rainfall areas. Dew fall is also an important source of moisture. Major river courses, such as that of the Orange River allow fog to advance deeper into the inland (DESMET & COWLING 1999). The mean annual air humidity is also higher along the costs (about 85% in Swakopmund) and decreases sharply further inland (WALTER 1986; WERGER 1986). These climatic conditions along the coast are particularly suitable for the lichen growth and favour the occurrence of lichen fields in different areas through the coastal Namib

(SCHIEFERSTEIN 1989; SCHIEFERSTEIN & LORIS 1992; JÜRGENS & NIEBEL-LOHMANN 1995). Isotherms predominantly run parallel to the coast and the mean annual temperatures vary from 16–23 °C. The highest values occur in areas with the highest degree of continentality.

The northern part of the transect is dominated by sandy soils being composed of arenosols and calcisols and having in general a low nutrient status. The savanna region has a luvisols/cambisol association, while the dry southern part of Namibia (Nama Karoo) is dominated by shallow leptosols and regosols. The winter rainfall region shows a range of shallow to deep developed soils, partly with high accumulation of soluble salts. With increasing winter rainfall the sandy soils of the Fynbos region have leaching effects and a low nutrient status. The average pH values (measured in water, 1:2.5 solution) of topsoil and water at the observatories follow in general the rain gradient along the transect but are also affected by the different substrates. They are low in northern Namibia (about between pH 4.5 and 5.5), by higher summer rainfall, and increase with decreasing summer rainfall in Southern Namibia and north-western South Africa, with pH values between 6 and 8, partly up to 9. It decreases again by increasing annual average precipitation, in the Fynbos biome (A. Petersen, pers. comm.).

These climatic differences are the cause for the occurrence of different phytochorological subdivisions over the study area: a Sudano-Zambezian Region in the north-east, characterized by dry forests and savannas; a Karoo-Namib Region; and a Cape Floristic Region in the south, mainly characterized by a fynbos vegetation. According to JÜRGENS (1991), two main units can be distinguished in the Karoo-Namib Region: the Succulent Karoo Region and the Nama Karoo Region. The Succulent Karoo Region comprises most of the coastal Namib and the former "Western Cape Domain" in the sense of WERGER (1986) extending southwards to the mouth of the Olifantsrivier (RSA), and is characterized by the dominance of leaf succulent chamaephytes. It has very high diversity and high level of endemism with regard to vascular plants, and is strongly related to the Cape element. The Nama Karoo region is floristically more heterogeneous and some areas have low diversity. It includes the Namaland Domain (Namib lowlands from Angola to the north-eastern Richtersveld, Namaland plateau, and in the south the Orange River valley from the eastern Richtersveld to the Pofadder-Upington region), with strong affinities to the Sudano-Zambezian Region, a Namib Subdomain (the dry inland desert or semi-desert region east of the Succulent Karoo), an Eastern Karoo Domain and a Damaraland-Kaokoland Domain. JÜRGENS (1991) reports that the Succulent Karoo Region can be described as an arid region with high oceanic influence with buffered extreme temperature and high relative air humidity in late night and early morning, while the Namaland Domain is characterized by more continental air-dry conditions and more extreme temperatures.

Material and methods

Soil-growing lichens have been studied thus far at 22 of the 33 study sites located along the BIOTA transect (Fig. 1, Table 1). Each study site, called "observatory" in the contest of the project since used for a long-term monitoring, has a defined surface of 1 km². Lichen specimens were collected for identification and prepared in the laboratory for herbarium conservation. Part of the material was sent to specialists for identification or confirmation. The identification and nomenclature of

cited species is based on the following works: ADLER (1990); BREUSS (1990, 1993, 1995); BÜDEL (1987); DEGELIUS (1974); EGEA (1989); ELIX (1993, 1997, 1999a, b, c); ESSLINGER (1986); GUDERLEY & LUMBSCH (1996); HAFELLNER (1982); HALE (1986, 1987a, b, 1990); KÄRNEFELT (1988); MORENO & EGEA (1991, 1992); NASH & ELIX (1987); NASH *et al.* (2002); SCHULTZ & BÜDEL (2002); TIMDAL (1984, 1991); TRINKAUS *et al.* (2001); WIRTH & VĚZDA (1975).

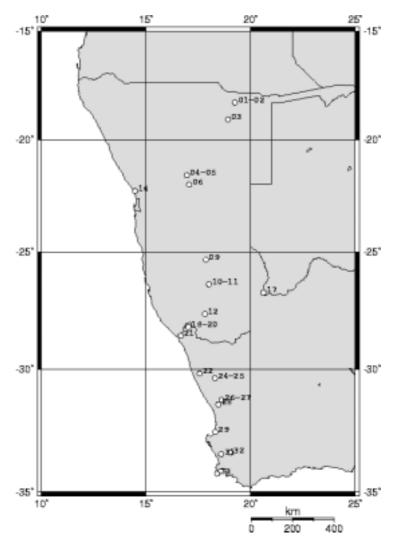


Fig. 1. Map of study area with location of all BIOTA observatories.

Some lichens were sterile, especially several species of the *Lichinaceae*, and could therefore not always be easily identified to species level; some others may entail new species (Table 2). Thin layer chromatography (TLC) was carried out to analyse the secondary compounds of most identified specimens, following the methodology of CULBERSON & KRISTINSSON (1970) and WHITE & JAMES (1985). Vouchers will be deposited in the herbarium of the Botanische Staatssammlung München (M) and in the National Herbarium Pretoria (PRE).

Collection data were databased using the *DiversityCollection*, a database application of the Diversity Workbench. Descriptive data on identified lichen species are entered in the *Lias Light* database, created with a selection of 72 diagnos-

tic characters. Both databases are consultable online via http://www.biotaafrica.org/1024/biota_south/structure_south.htm. A matrix with binary data was submitted to cluster analysis, using the Jaccard distance measure of similarity and the single link as clustering algorithm. Observatories with less than 3 species were not considered in the cluster analysis. Only lichens growing on soil or partly on soil and partly on pebbles were considered in this elaboration.

Table 1. The observatories and their vegetation types

Namibia

- 01) Mile 46 Research Station, 18° 8' S, 19° 15' E, northern Kalahari dry woodland vegetation.
- 02) Mutompo, 18° 8' S, 19° 15' E, northern Kalahari dry woodland vegetation.
- 03) Sonop, 19° 04' S, 18° 54' E, northern Kalahari dry woodland vegetation.
- 04) Toggerkry 250, 21° 30' S, 16° 43' E, thorn-bush savannah vegetation.
- 05) Otjimongombe West 44, 21° 35′ S, 16° 56′ E, thorn-bush savannah vegetation.
- 06) Okamboro, 22° 01′ S, 17° 03′ E, highland savannah vegetation.
- 08) Niko 377, 25° 20' S, 17° 50' E, dwarf shrub savannah vegetation.
- 10) Gellap Ost 3, 26° 24' S, 18° 00' E, dwarf shrub savannah vegetation (Nama-Karoo).
- 11) Nabaos 7, 26° 23' S, 17° 59' E, dwarf shrub savannah vegetation (Nama-Karoo).
- 12) Fish River Canyon, 27° 41' S, 17° 48' E, dwarf shrub savannah vegetation (Nama-Karoo).
- 16) Myl 14 (Wlotzkasbaken), 22° 18' S, 14° 28' E, lichen field.

Republic of South Africa

- 17) Alpha, 26° 45′ S, 20° 36′ E, Kalahari thornveld vegetation.
- 18) Koeroegapvlakte, 28° 14' S, 17° 01' E, Succulent Karoo vegetation.
- 20) Numees, 28° 18' S, 16° 57' E, Succulent Karoo vegetation.
- 21) Groot Derm 10, 28° 36′ S, 16° 39′ E, Succulent Karoo vegetation.
- 22) Quaggafontein 478, 30° 11′ S, 17° 33′ E, Succulent Karoo lowland vegetation and Namaqualand rocky hill vegetation.
- 24) Leliefontein 624, 30° 23' S, 18° 17' E, upland Succulent Karoo and fynbos vegetation.
- 25) Remhoogte 416, 30° 23' S, 18° 17' E, upland Succulent Karoo and fynbos vegetation.
- 26) Flaminkvlakte 111, 31° 17′ S, 18° 36′ E, quartz field, Succulent Karoo vegetation.
- 27) Luiperskop, 31° 17′ S, 18° 36′ E, quartz field, Succulent Karoo vegetation.
- 28) Moedverloren 208, 31° 27′ S, 18° 26′ E, quartz field, Succulent Karoo vegetation.
- 29) Roscherpan Nature Reserve, 32° 36′ S, 18° 18′ E, strandveld, transition between Succulent Karoo and lowland fynbos vegetation.

Results and discussion

A total of 59 terricolous lichen species have been hitherto recorded along the transect. Only 12 of the 22 examined observatories host soil-growing lichens (Table 2). The recorded species belong to 24 genera from 14 families. The most widespread species are *Psora* sp. 1 (8 observatories), *Placidium squamulosum*{ XE "*Placidium: P. squamulosum* (Ach.) Breuss " } (5 observatories) and *P. tenellum*{ XE "*Placidium: P. tenellum* (Breuss) Breuss" } (6 observatories). The most frequently present genera are Xanthoparmelia (8 species), *Diploschistes* (5 species), *Toninia* (5 species) and *Placidium* (4 species), and the most frequent families are *Parmeliaceae* (11 species), *Lichinaceae* (8 species), *Catillariaceae, Verrucariaceae, Thelotremataceae* and *Teloschistaceae* (5 species each).

Collema texanum{ XE "Collema: C. texanum Degelius" }, Diploschistes cf. thelenelloides{ XE "Diploschistes: D. cf. thelenelloides Lumbsch & Aptroot" }, Lecanora pseudis*tera{ XE "Lecanora: L. pseudistera* Nyl." *}, Peccania* aff. *fontequeriana{ XE "Peccania: P.* aff. *fontequeriana* P. P. Moreno & Egea" *}, Placidium lacinulatum{ XE "Placidium: P. lacinu-latum* (Ach.) Breuss " *}* and *Toninia* aff. *ruginosa{ XE "Toninia: T.* aff. *ruginosa* (Tuck.) Herre" *}* are reported for the first time from Southern Africa. New species of Siphula (KANTVILAS *et al.* 2003), and *Buellia* (GRUBE & ZEDDA in prep.) were or will be described as new to science.

The examined lichen mycota is particularly rich when compared with that of other arid to semi-arid environments. According to ROGERS (1977), the global diversity of lichens in deserts includes 947 species, growing on all kinds of substrates, while ELDRIDGE (2001) estimates the world-wide lichen and bryophyte diversity of biological soil crusts in arid and semiarid regions to be about 250 species. ROGERS (1972a, b) and ROGERS & LANGE (1972) report 42 lichen taxa from soil surfaces within an area of one million square kilometres in south-eastern Australia. ELDRIDGE (1996) reports 48 taxa from an area of 60000 km² in western New South Wales. According to ELDRIDGE (2001), the lichen crust mycota of Australia shows strong similarities with other arid landscapes worldwide. The most common genera in arid and semiarid parts of Australia are Acarospora, Endocarpon, Placidium, Diploschistes, Peltula and Xanthoparmelia. All of these except for Endocarpon were also found in Southern Africa. Eighty-two genera of lichens are reported by BÜDEL (2001) from biological soil crusts worldwide, 44 of which are found in North America, 34 in Europe, 19 in Africa, 16 in the Middle East, 24 in Asia and 26 in Australia.

Observatorium No.	03	08	16	18	20	21	22	24	25	26	27	28	Presence
Acarospora sp. 01					1								1
Acarospora sp. 02											1		1
Acarospora sp. 03{ XE "Acarospora: A. sp. " }			1										1
<i>Buellia</i> sp. 01 <i>{ XE "Buellia: B.</i> sp. " <i>}</i>							1				1		2
Buellia sp. 02										1		1	2
Buellia sp. 03			1										1
Buellia sp. 04					1								1
Caloplaca elegantissima{ XE "Caloplaca: C. elegantissima (Nyl.) Zahlbr." } (Nyl.) Zahlbr.			1										1
Caloplaca volkii{ XE "Caloplaca: C. volkii	·	•	I	•	•	·	·	·	·	•	•	·	I
V. Wirth & Vězda" } V. Wirth & Vězda			1										1
Caloplaca sp. 01{ XE "Caloplaca: C. sp. "							1			1	1	1	4
/ Caloplaca sp. 02 { XE "Caloplaca: C. sp. "	·	•	•	•	•	•	I	•	•	I	I	I	4
										1	1		2
Collema sp. 01 { XE "Collema: C. sp. " }							1						1
Collema texanum{ XE "Collema: C. texa-													
num Degelius" } Degelius					1								1
Diploschistes sp. 01 { XE "Diploschistes: D. sp. " }			1										1
Diploschistes actinostomus{ XE "Diplos- chistes: D. actinostomus (Pers. ex				1						•			1

Table 2. Diversity of soil-growing lichens at the examined observatories.

Ach.) Zahlbr. " } (Pers. ex Ach.) Zahlbr .													
Diploschistes aeneus { XE "Diploschistes:													
D. aeneus (Müll. Arg.) Lumbsch" } (Müll.													
Arg.) Lumbsch					1								1
Diploschistes hensseniae{ XE "Diplo-													
schistes: D. hensseniae Lumbsch &													•
Elix" } Lumbsch & Elix	•	•	•	·	·	·	•	·	·	1	1	·	2
Diploschistes cf. thelenelloides { XE "Diplo- schistes: D. cf. thelenelloides Lumbsch													
& Aptroot" } Lumbsch & Aptroot					1								1
Lecanora pseudistera { XE "Lecanora: L.	•	•	·	·		·	·	·	•	•	·	·	'
pseudistera Nyl." } Nyl.				1									1
Lecidella crystallina { XE "Lecidella: L.													
crystallina V. Wirth & Vĕzda" } V. Wirth &													
Vězda	•	•	1										1
Lempholemma sp. 01{ XE "Lempholem-					4								4
ma: L. sp. " }	•	•	•	·	1	·	•	·	·	;	·	·	1
Lichinales sp. 01	•	•	•	•	·	·	·	·	·		·	·	1
Lichinella sp. 01{ XE "Lichinella: L. sp. " }	•	·	·	·	·	·	÷	·	·	1	·	·	1
Neofuscelia sp. 01	•	·	·	·	·	·	1	·	·	·	·	·	1
Neofuscelia aff. imitatrix { XE "Neofuscelia:													
<i>N.</i> aff. <i>imitatrix</i> (Taylor) Essl." } (Taylor) Essl.										1			1
Paraparmelia prolata { XE "Paraparmelia:	•	•	•	•	•	•	•	•	•	1	•	•	
<i>P. prolata</i> (Hale) Elix & J. Johnst." } (Ha-													
le) Elix & J. Johnst.										1			1
Peltula coriacea { XE "Peltula: P. coriacea													
Büdel, Henssen & Wessels" } Büdel,													
Henssen & Wessels	•	•			1								1
Peltula inversa{ XE "Peltula: P. inversa													
Büdel, & Schultz" } Büdel & M. Schultz	•	1	·	·	•	·	·	·	·	·	·	·	1
Peccania aff. cerebriformis { XE "Peccania: P. aff. cerebriformis Henssen & Büdel" }													
Henssen & Büdel							1						1
Peccania aff. fontequeriana { XE "Peccania:	•	•	·	·	•	·	'	·	•	•	·	·	'
<i>P.</i> aff. fontequeriana P. P. Moreno &													
Egea" } P. P. Moreno & Egea					1					1			2
Peccania sp. 01 <i>{ XE "Peccania: P.</i> sp. " <i>}</i>					1								1
Placidium lacinulatum{ XE "Placidium: P.													
<i>lacinulatum</i> (Ach.) Breuss " } (Ach.)													
Breuss	1	•	•	•	•	•	•	•	•	·	•	•	1
Placidium semaforonense { XE "Placidium:													
P. semaforonense (Breuss) Breuss " } (Breuss) Breuss				1									1
Placidium squamulosum{ XE "Placidium:	•	•	·		•	·	·	·	•	•	·	·	'
<i>P. squamulosum</i> (Ach.) Breuss " }													
(Ach.) Breuss					1			1	1	1	1		5
Placidium tenellum{ XE "Placidium: P.													
<i>tenellum</i> (Breuss) Breuss" } (Breuss)													
Breuss	•	•	•	·	1	·	1	•	1	1	1	1	6
Protoparmelia sp. 01{ XE "Protoparmelia:					1								1
P. sp. " } Psora aff. cerebriformis{ XE "Psora: P. aff.	•	•	•	•	I	·	•	·	·	·	·	·	I
cerebriformis W. A. Weber" } W. A.													
Weber										1			2
Psora crenata{ XE "Psora: P. crenata			-	-		-	-	-		-	•	-	-
(Taylor) Reinke" } (Taylor) Reinke					1					1			1
Psora sp. 01					1	1	1	1	1	1	1	1	8
Ramalina capensis{ XE "Ramalina: R.			1										1

<i>capensi</i> s Th. Fr." } Th. Fr .													
Sarcogyne sp. 01 { XE "Sarcogyne: S. sp. "													
}							1					1	2
Siphula flavovirens{ XE "Siphula: S.													
flavovirens Kantvilas, Zedda & Elix" }													
Kantvilas, Zedda & Elix							1						1
Teloschistes capensis{ XE " Teloschistes:													
<i>T. capensis</i> (L. f.) Müll. Arg." } (L. f.) Müll .													
Arg.			1										1
Toninia australis{ XE "Toninia: T. australis													
Timdal" } Timdal												1	1
Toninia lutosa { XE "Toninia: T. lutosa													
(Ach.) Timdal" } (Ach.) Timdal					1		1			1			3
Toninia aff. lutosa { XE "Toninia: T. aff.													
<i>lutosa</i> (Ach.) Timdal" } (Ach.) Timdal					1							1	2
Toninia aff. ruginosa { XE "Toninia: T. aff.													
ruginosa (Tuck.) Herre" } (Tuck.) Herre							1			1			2
Toninia sp. 01 { XE "Toninia: T. sp. " }			1							1	1	1	4
Thyrea sp. 01 { XE "Tyrea: T. sp. " }										1			1
<i>Thyrea</i> sp. 02 { <i>XE</i> " <i>Tyrea: T</i> . sp. " }					1								1
Verrucaria compacta { XE "Verrucaria: V.	•	•	•	•	•	•	•	•	•	•	•	•	1
compacta (A. Massal.) Jatta" } agg.										1			1
Xanthoparmelia amphixanthoides { XE "Xan-	•	•	•	•	•	•	•	•	·		•	•	
thoparmelia: X. amphixanthoides													
(Steiner & Zahlbr.) Hale" } (J. Steiner &													
Zahlbr.) Hale										1			1
Xanthoparmelia crassilobata { XE "Xantho-	•	•	•	•	•	•	•	•	·	•	•	•	•
parmelia: X. crassilobata Hale" } Hale										1			1
Xanthoparmelia epigea { XE "Xanthopar-	•	•	•	•	•	•	•	•	·	•	•	•	•
<i>melia:</i> X. epigea Hale" } Hale												1	1
Xanthoparmelia hyporhytida { XE "Xantho-	•	•	•	•	•	•	•	•	•	•	·		
<i>parmelia:</i> X. hyporhytida (Hale) Hale" }													
(Hale) Hale										1			1
Xanthoparmelia leonora	-	•	•	•	•	•	•	•	•	•	•	•	•
<i>{ XE "Xanthoparmelia: X. leonora</i> (A.													
Massal.) Hale" } (A. Massal.) Hale										1	1	1	3
Xanthoparmelia simulans{ XE "Xantho-													
parmelia: X. simulans Hale" } Hale										1			1
Xanthoparmelia walteri{ XE "Xanthoparme-													
lia: X. walteri M. D. E. Knox" }													
M. D. E. Knox			1										1
Xanthoparmelia sp. 01 { XE "Xanthoparme-													
<i>lia:</i> X. sp. " }										1			1
	-	-	0	ŝ	~	-	-	7	e	ŝ	0	6	
Number of species	•	•	Ŧ	•••	-	•	÷	••	••	25	Ŧ	9	

As shown in Table 2 and in Fig. 2, soil-growing lichens are most frequent and abundant in regions with a winter rain system, especially in Namaqualand (observatories 18–28) rather than in regions of summer rain. Diversity decreases again in the Fynbos biome (observatory 29), probably due to sandy soil and to the higher coverage degree of shrubs, which create unfavourable light conditions for the growth of soil lichens. Fynbos vegetation is moreover frequently subject to fire. The observatory 26 (Flaminkvlakte 111, Goedehoop) has the highest diversity of terricolous lichens (25 taxa/km²), followed by the observatories 20 (Richtersveld Park, Numees with 17 taxa/km²) and 22 (Quaggafontein 478, Soebatsfontein, with 11 taxa/km²). Also two other observatories located in the Knersvlakte have a high diversity (obs. 27, 28) with 10 taxa/km² each.

As can be seen from the graph of the mean annual precipitation (Fig. 3), it appears that lichen diversity is negatively correlated to the quantity of precipitation. At higher precipitation levels (350–550 mm) none to very few terricolous lichen species are found, and the distribution of these by low precipitation (< 350 mm) is variable. That means that other ecological factors are more important for the lichen diversity. In Fig. 3, observatories are sorted according to the air distance from the coast, measured on a map. According to different authors (e.g. GOTZ-MANN 2002), this is an indirect measure of fog and air humidity since localities located closer to the coast are more subject to the effects of the Benguela Current. As shown in the diagram, the lichen mycota is much more diverse close to the coast (observatories 16, 18, 20, 22, 26, 27, 28), with the exception of the observatories 21 and 29 which are characterized by a sandy soil (arenosol), an unsuitable substrate for lichens due to instability. Because of the favourable climate, soil-growing lichens could potentially grow here, but are in fact absent or very rare. Therefore, in this case, the soil type seems to be an additional more important factor for lichen distribution.

Comparable results are reported from other arid areas as well. In south-eastern Australia the richness of soil-surface lichens follows a rainfall gradient, increasing with higher amounts of rainfall and showing clear floristic patterns of arid and semi-arid species (ROGERS 1977). ELDRIDGE (2001) reports that the lichen coverage is reduced in areas of Australia dominated by summer rainfall, where coverage and species diversity of cyanobacteria increase, whereas the highest lichen diversity is found in winter rain areas. In North America similar patterns are found, with an influence of seasonal precipitation on the dominance and distribution of biological soil crusts. According to BELNAP *et al.* (2001), ecoregions that receive summer rain (e.g. the Sonoran Desert) tend to have a greater diversity of heterocystic cyanobacteria and lower lichen abundance.

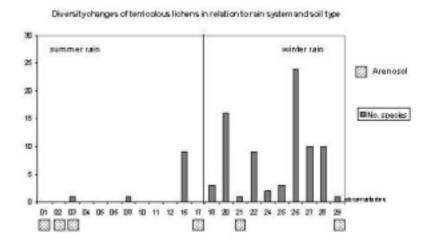


Fig. 2. Diversity change of terricolous lichens in relation to rain system and soil type (observatories sorted according to their location from the north to the south).

In these areas the most common lichen genera are *Collema*, *Placidium* and *Peltula*. The latter two genera were also found in the summer rain observatories of Namibia. In cool deserts and in deserts with winter rainfall (e.g. Mojave and Great

Basin in the Southwestern U.S.A.), crusts are richer in lichen species (BELNAP *et al.* 2001).

As pointed out by BELNAP *et al.* (2001), calcareous and gypsiferous soils as well as more stable, fine-textured soils generally support higher coverage of species-rich crusts with some taxa being excellent indicators of soil chemistry (e.g. of the content of calcium carbonate), while on more unstable soils, lichens and mosses may be found only below vascular plants. Shallow soils support a wider variety of lichens, regardless of soil texture. Also ELDRIDGE (1996) reports a great species diversity from plains in Australia with calcareous earths (38 taxa) and from those with red earths (11.2 taxa in mean value).

In Southern Australia lichens are mostly restricted to loamy soils and are absent from cracking and swelling clays and on sandy soils (ELDRIDGE 2001). In the Namib desert the distribution of the lichen fields is conditioned by the lack of dunes and the presence of a stable, gravel plain, while lichens are much rarer in dry river beds, salt pans and sand dunes (SCHIEFERSTEIN & LORIS 1992). More lichens are also found in Southern Africa at those observatories with a greater stone coverage or rocky surface (20, 26, 27, 28). According to BELNAP *et al.* (2001) and ROSENTRETER & BELNAP (2001), stable or embedded rocks near or at soil surface can increase the percent crust cover by perching water and protecting the surface from physical disturbance.

In some of the investigated observatories the absence or lower abundance of soil-growing lichens may also be related to man-made disturbance. Future analyses will focus on this aspect.

With respect to growth-form, most species are crustose (34%) and foliose (30.5%), including small foliose forms (Fig. 4). Crustose and squamulose growth-forms, seemingly best adapted to aridity (see further below), account to 56% of the species collected. Fruticose (10.2%, including small fruticose), placoid (1.7%) and peltate (1.7%) lichens are less frequent. Other growth-forms (e.g. leprose or endolithic thalli) are not represented in the mycota. The distribution of growth-forms at the different observatories, indicates that crustose and squamulose lichens are the most widespread through all the examined observatories. Foliose and fruticose lichens are only found at those observatories located closer to the coast where air humidity is higher and fog events are more frequent (16, 20, 22, 26, 27, 28). These last two growth-forms can be therefore considered as good indicators of increased air humidity.

According to several authors (ROGERS 1977; ELDRIDGE 2001), crustose and squamulose lichens are dominant in arid regions since their reduced surface area is an adaptation which permits survival under arid conditions. BELNAP *et al.* (2001) report that biological soil crusts in regions influenced by fog in North America support the greatest amount of fruticose lichens. ELDRIDGE (1996) notes 74% of crustose lichens in the lichen mycota of New South Wales (Australia), and reports that 43% of soil lichens from Australia are foliose or fruticose (ELDRIDGE 2001).

The cluster analysis shown in Fig. 5 indicates that floristically most distinct are the observatories 18, in the Richtersveld area, and 16 in the Namib desert. Observatory 20, which is also located in the Richtersveld area, shows low similarity to the other clusters of observatories (about 20%). Observatories 24 and 25, which are directly neighboured to each other, and separated only by a fence, show

greater similarities (about 70%). They are characterized by two different land use systems. One observatory is located on heavily grazed communal land, while the other is part of an extensively grazed commercial farm (TODD & HOFFMAN 1999).

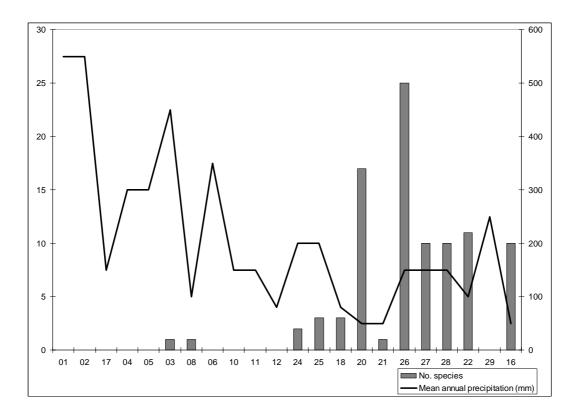


Fig. 3. Diversity change of terricolous lichens in relation to mean annual precipitation (observatories sorted according to decreasing air distance from the coast).

With regard to higher plants, the species diversity of the two observatories is similar, but the floristic composition exhibits many differences, with more annuals and geophytes being present in the heavily grazed area, while shrubs and leaf succulents are more frequent on land with less grazing impact. However, the soil lichen composition and diversity in both observatories, apparently shows no differences. This might be due to the fact that lichens need more time to differentiate after the impact of man-made disturbance. Observatories 27 and 28 are both located in the quartz fields of the Knersvlakte and show greater affinity (about 35%) to each other than to the nearby observatory 26. Both these observatories are more disturbed than 26, which is located on a commercial farm and exhibits greater diversity. The observatory 27 is on a communal land and affected by more intense grazing than 26. Observatory 28 was heavily grazed by sheep until end of 2001 and now has the status of a WWF nature reserve. Observatory 22, which is located between the Richtersveld area and the Knersvlakte, and near to observatories 24 and 25, has low similarity with the flora of these other areas.

Conclusion

In the present study, clear differences in species richness and composition of soil-inhabiting lichens, as well as in the distribution of growth-forms were found along the transect between summer and winter rain areas. This clearly indicates the bioindicative value of lichens for estimating climatic changes in Southern Africa. As already pointed out by BELNAP *et al.* (2001), certain arid areas of the world that are currently winter rain dominated are predicted to receive increased summer rain in the future, a situation, which most likely will also concern Southern Africa as a consequence of global climatic change.

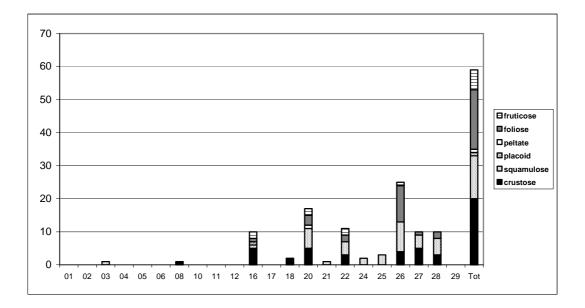


Fig. 4. Growth-form occurrence in the entire terricolous lichen mycota (Total) and in that of the single observatories (01–29).

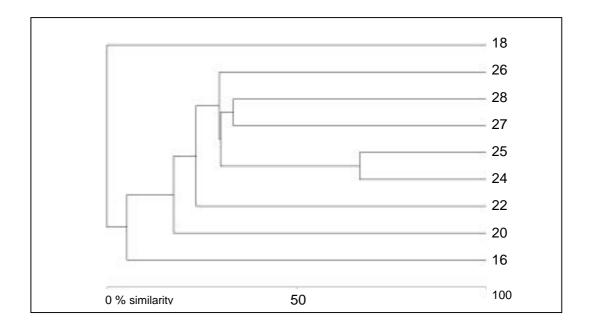


Fig. 5. Cluster analysis of the examined terricolous lichen mycota at the different observatories, using the Jaccard distance measure of similarity and the single link as clustering algorithm.

Due to a reduction of lichen diversity, especially of soil-inhabiting species, this effect might be reflected in a shift in soil crust composition. Soil-growing lichens also appear to be suitable indicators of soil types since they are usually not found on unstable substrates. Furthermore, the intensity of man-made disturbance is an important factor affecting terricolous lichen diversity. Comparing closely adjacent observatories with different land use systems (commercial farms versus community land), the loss of diversity in more intensively grazed areas (community land) becomes clearly evident and it can be shown, that the lichen mycobiota responds very slowly to cessation of disturbance due to nature conservation policies, and that lichen recovery appears much slower in comparison to higher plants. Lichens can therefore also be considered suitable indicators for the intensity of man-made disturbance in Southern Africa.

Acknowledgments

We thank the Ministries of Environment and Tourism (MET) and of Agriculture, Food and Fisheries (MAFF) in Namibia, the Northern Cape Nature Conservation, the Western Cape Nature Conservation Board, the Richtersveld National Park, the Cape Peninsula National Park in the Republic of South Africa, as well as landowners and communities in Namibia and RSA, for granting collection and export permits. The Federal Ministry for Education and Research of Germany (BMBF) is thanked for financial support. We are also indebted to all BIOTA co-workers, especially to A. Petersen, for useful information on the observatories (soil, climate, vegetation) and for providing logistics, and to U. Sukopp for support during fieldwork. For identifying specimens, we would like to thank O. Breuss (*Placidium*), J. A. Elix (*Siphula*), U. Grube (*Buellia*), J. Hafellner (*Caloplaca, Sarcogyne*), G. Kantvilas (*Siphula*), H. T. Lumbsch (*Diploschistes*), and E. Timdal (*Psora*). G. Kantvilas is kindly thanked for comments and corrections on this paper.

References

- ADLER, M. T. (1990): An artificial key to the genera of the *Parmeliaceae* (Lichens, *Ascomycotina*). *Mycotaxon* **38:** 331–347.
- BELNAP, J., & LANGE, O. L. (eds) (2001): Biological Soil Crusts: Structure, Function and Management. *Ecological Studies* 150: 1–503.
- BELNAP, J., KALTENECKER, J. H., ROSENTRETER, R., WILLIAMS, J., LEONARD, S. & EL-DRIDGE, D. (2001): *Biological Soil Crusts: Ecology and Management*. USDI, Bureau of Land Mangement. Technical Reference 1730-2. Denver, CO. 110 pp.
- BREUSS, O. (1990): Die Flechtengattung *Catapyrenium (Verrucariaceae)* in Europa. *Stapfia* 23: 1–153.
- BREUSS, O. (1993): Studien über die Flechtengattung *Catapyrenium* (*Verrucariaceae*). V. Einige Arten aus dem südlichen Afrika. *Linzer Biologische Beiträge* **25**: 339–346.
- BREUSS, O. (1995): The genus *Catapyrenium* (*Verrucariales*) in the Southern Hemisphere. *Cryptogamic Botany* **5**: 177–183.

- BÜDEL, B. (1987): Zur Biologie und Systematik der Flechtengattungen Heppia und Peltula im südlichen Afrika. Bibliotheca Lichenologica 23: 1–105.
- BÜDEL, B. (2001): Comparative Biogeography of Soil-Crusts Biota. In: BELNAP, J. & LANGE, O. L. (eds), Biological Soil Crusts: Structure, Function and Management. *Ecological Studies* 150: 141–152.
- CULBERSON, C. F. & KRISTINSSON, H. (1970): A standardized method for the identification of lichen products. *Journal of Chromatography* **46:** 85–93.
- DEGELIUS, G. (1974): The lichen genus *Collema* with special reference to the extra-European species. *Symbolae Botanicae Upsaliensis* **20**: 1–215.
- DESMET, P. G. & COWLING, R. M. (1999): The climate of the Karoo a functional approach. In: RICHARD, W., DEAN, J. & MILTON, S. J. (eds), *The Karoo. Ecological patterns and processes*, p. 3–16. Cambridge University Press.
- EGEA, J. M. (1989): Los géneros *Heppia* y *Peltula* (Líquenes) en Europa Occidental y Norte de África. *Bibliotheca Lichenologica* **31**: 1–122.
- ELDRIDGE, D. J. (1996): Distribution and floristics of terricolous lichens in soil crusts in arid and semi-arid New South Wales, Australia. *Australian Journal of Botany* **44**: 581–599.
- ELDRIDGE, D. J. (2001): Biological soil crusts of Australia. In: BELNAP, J. & LANGE, O. L. (eds), Biological Soil Crusts: Structure, Function and Management. *Ecological Studies* 150: 119–131.
- ELIX, J. A. (1993): Progress in the generic delimitation of *Parmelia sensu lato* Lichens (*Ascomycotina: Parmeliaceae*) and a synoptic key to the *Parmeliaceae*. *The Bryologist* **96**: 359–383.
- ELIX, J. A. (1997): New species and new combinations in the lichen family *Parmeliaceae* (*Ascomycotina*) from South Africa. *Mycotaxon* **63**: 335–343.
- ELIX, J. A. (1999a): Further new species and new reports in the lichen family *Parmeliaceae* (*Ascomycotina*) from South Africa. *Mycotaxon* **70**: 103–110.
- ELIX, J. A. (1999b): New species of *Neofuscelia* (lichenized *Ascomycotina, Parmeliaceae*) from the Southern Hemisphere. *Mycotaxon* **71**: 431–456.
- ELIX, J. A. (1999c): New species of *Xanthoparmelia* (lichenized *Ascomycotina*, *Parmeliaceae*) from South Africa. *Mycotaxon* **73**: 51–61.
- ESSLINGER, T. L. (1986): Further reports on the brown *Parmeliaceae* of southern Africa. *Nordic Journal of Botany* **6**: 87–91.
- GOTZMANN, I. H. (2002): Vegetationsökologie und Vegetationsdynamik im Richtersveld (Republik Südafrika). – Inaugural-Dissertation zur Erlangung des Doktorgrades der Mathematisch-Naturwissenschaftlichen Fakultät der Universität Köln, p. 1–135.
- GUDERLEY, R. & LUMBSCH, H. T. (1996): The lichen genus *Diploschistes* in South Africa (*Thelotremataceae*). Mycotaxon 58: 269–292.
- HAFELLNER, J. (1982): Caloplaca bellemerei, eine weitere pluriloculäre Caloplaca-Art (Lichenes, Lecanorales) aus Australien. Herzogia 6: 283–287.
- HALE, M. E. (1986): New species of the lichen genus *Xanthoparmelia* from southern Africa (*Ascomycotina: Parmeliaceae*). *Mycotaxon* 27: 563–610.
- HALE, M. E. (1987a): Additions to the *Xanthoparmelia* flora of southern Africa (Lichenized Ascomycotina: Parmeliaceae). Mycotaxon 29: 251–266.
- HALE, M. E. (1987b): New or interesting species of Xanthoparmelia (Vainio) Hale (Ascomycotina: Parmeliaceae). Mycotaxon 30: 319–334.
- HALE, M. E. (1990): A synopsis of the lichen genus *Xanthoparmelia* (Vainio) Hale (*Ascomycotina, Parmeliaceae*). *Smithsonian Contributions to Botany* **74:** 1–250.
- JÜRGENS, N. (1991): A new approach to the Namib Region. I: Phytogeographic subdivision. Vegetatio 97: 21–38.
- JÜRGENS, N. & NIEBEL-LOHMANN, A. (1991): The unknown lichen hill. Veld & Flora 77: 24–26.
- JÜRGENS, N. & NIEBEL-LOHMANN, A. (1995): Geobotanical observations on lichen fields of the southern Namib desert. *Mitteilungen aus dem Institut f
 ür Allgemeine Botanik Hamburg* 25: 135–156.
- KANTVILAS, G., ZEDDA, L. & ELIX, J. A. (2003): A remarkable new species of *Siphula* (lichenized fungi) from South Africa. *Herzogia* 16: 21–25.

- KÄRNEFELT, I. (1988): Morphology and biogeography of saxicolous *Caloplaca* in southern Africa. *Monographs in Systematic Botany from the Missouri Botanic Garden* **25**: 439–452.
- MORENO, P. P. & EGEA, J. M. (1991): Biología y taxonomía de la familia *Lichinaceae*, con especial referencia a las especies del S. E. España y Norte de África. *Universidad de Murcia, Secretariado de Publicaciones*. 87 pp.
- MORENO, P. P. & EGEA, J. M. (1992): Estudios sobre el complejo Anema-Thyrea-Peccania en el sureste de la Península Ibérica y norte de Africa. Acta Botanica Barcinonensia **41**: 1–66.
- NASH III, T. H. & ELIX, J. A. (1987): New species and new reports in the *Parmeliaceae* (Lichenized *Ascomycotina*) from South Africa and Australia. *Mycotaxon* **29**: 467–476.
- NASH III, T. H., RYAN, B. D., GRIES, C. & BUNGARTZ, F. (eds) (2002): Lichen Flora of the Greater Sonoran Desert Region 1. Lichens Unlimited, Arizona State University, Tempe, Arizona. 532 pp.
- ROGERS, R. W. (1972a): Soil surface lichens in arid and sub-arid south-eastern Australia. II. Phytosociology and geographic zonation. *Australian Journal of Botany* **20**: 215–227.
- ROGERS, R. W. (1972b): Soil surface lichens in arid and sub-arid south-eastern Australia. III. The relationship between distribution and environment. *Australian Journal of Botany* **20**: 301–316.
- ROGERS, R. W. (1977): Lichens of hot arid and semi-arid lands. In: SEAWARD, M. R. D. (ed.), *Lichen Ecology*, p. 211–252. Academic Press, London, New York, San Francisco.
- ROGERS, R. W. & LANGE, R. T. (1972): Soil surface lichens in arid and sub-arid south-eastern Australia. I. Introduction and floristics. *Australian Journal of Botany* **20**: 197–213.
- ROSENTRETER, R. & BELNAP, J. (2001): Biological soil crusts of North America. In: BELNAP, J. & LANGE, O. L. (eds), Biological Soil Crusts: Structure, Function and Management. *Ecological Studies* 150: 31–50.
- SCHIEFERSTEIN, B. (1989): Ökologische Untersuchungen an den Flechtenfeldern der Namib-Nebelwüste, p. 1–180. Diplomarbeit, Universität Stuttgart-Hohenheim.
- SCHIEFERSTEIN, B. & LORIS, K. (1992): Ecological investigations on lichen fields of the Central Namib. I. Distribution patterns and habitat conditions. *Vegetatio* 98: 113–128.
- SCHULTZ, M. & BÜDEL, B. (2002): Key to the genera of the *Lichinaceae*. *Lichenologist* 34: 39–62.
- TIMDAL, E. (1984): The delimitation of *Psora* (*Lecideaceae*) and related genera, with notes on some species. *Nordic Journal of Botany* **4**: 525–540.
- TIMDAL, E. (1991): A monograph of the genus *Toninia* (*Lecideaceae*, *Ascomycetes*). *Opera Botanica* **110**: 1–137.
- TODD, S. W. & HOFFMAN, M. T. (1999): A fence-line contrast reveals effects of heavy grazing on plant diversity and community composition in Namaqualand, South Africa. *Plant Ecology* 142: 169–178.
- TRINKAUS, U., MAYRHOFER, H. & ELIX, J. A. (2001): Revision of the *Buellia epigaea*-group (lichenized Ascomycetes, Physciaceae) 2. The species in Australia. Lichenologist 33: 47– 62.
- ULLMANN, I. & BÜDEL, B. (2001): Biological soil crusts of Africa. In: BELNAP, J. & LANGE, O. L. (eds), Biological Soil Crusts: Structure, Function and Management. *Ecological Studies* 150: 107–118.
- WALTER, H. (1986): The Namib desert. In: EVERNARI, M., NOY-MEIR, I. & GOODALL, D. W. (eds), Hot deserts and arid shrublands. *Ecosystems of the World* 12 B, **284**: 245–282.
- WERGER, M. J. A. (1986): The Karoo and southern Kalahari. In: EVERNARI, M., NOY-MEIR, I. & GOODALL, D. W. (eds), Hot deserts and arid shrublands. *Ecosystems of the World* 12 B, 284: 283–359.
- WEST, N. E. (1990): Structure and function of soil microphytic crusts in wildland ecosystems of arid and semi-arid regions. *Advances in Ecological Research* **20**: 179–223.
- WHITE, F. J. & JAMES, P. W. (1985): A new guide to microchemical techniques for the identification of lichen substances. *British Lichen Society Bulletin* **57**, Suppl.: 1–41.
- WIRTH, V. & VĚZDA, A. (1975): Drei neue Flechtenarten aus Südwestafrika. *Stuttgarter Beiträge zur Naturkunde*, Ser. A, **284:** 1–4.