Terricolous lichens in the northern Namib Desert of Namibia: Distribution and community composition

Article *in* The Lichenologist · January 2005

DOI: 10.1017/S0024282904014203

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The Lichenologist **37**(1): 77–91 (2005)
DOI: 10.1017/S0024282904014203 *Printed in the United Kingdom*

Terricolous lichens in the northern Namib Desert of Namibia: distribution and community composition

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Abstract: Terricolous lichens are the dominant vegetation in expansive areas of the Namib Desert, where fog is the main source of moisture and other vegetation is scarce. They play several important roles in soil crust stabilization and in the primary production of the Namib Desert ecosystem, yet little is known about the diversity and distribution of lichens in the northern unexplored regions of the Namib. To our knowledge, this study is the first survey of terricolous lichens to be carried out in the northern Namib Desert. Seven soil crust habitat types were identified in the study area, and a total of twenty-eight soil crust lichen species was recorded. The survey uncovered lichen species that may be unique to the northern Namib, including vagrant species, and common species were frequently found in a vagrant form. The crustose group was the most widely represented. Overall community compositions differed from those found in other regions of the Namib, and distribution patterns suggest a link to gravel clast size and physical soil crust type.

Key words: biological soil crust, desert lichens, lichen distribution, Skeleton Coast

Introduction

The biologically unexplored regions of the Namib Desert in Namibia are potentially threatened due to a change in land use with expanding mining activities and increasing tourism. There have been few scientific assessments of the biodiversity in the northern Namib Desert, and we know of no other work on the unique, ground-dwelling lichen communities of this region that have been shown to be extremely sensitive to disturbance in the central Namib (Wessels & van Vuuren 1986). In the past, this region of the Namib Desert has been inaccessible to scientists due to its remote location and its status as a restricted area of Skeleton Coast Park, so that previous work on lichens in the Namib has focused primarily on the central Namib. Here, we report the first survey of terricolous lichens in the northern Namib Desert in an effort to improve knowledge of these ecologically and geomorphically important components of this unique fog desert.

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Lichens in the Namib Desert grow in dense and diverse communities on rocks, trees and as part of biological soil crusts. The main biotic components of biological soil crusts in the Namib are cyanobacteria, algae, and lichens; lichens being the most visible and prolific. The importance of soil crust lichens has been recognized in arid regions around the globe. The micro-flora of biological crusts help to bind sediments and provide a stable environment for the higher trophic levels in arid land ecosystems (Campbell *et al.* 1989). Because biological crusts often occur in vast areas devoid of higher plants, they make significant contributions to primary production in arid environments, serving as nitrogen sources and converters of CO_2 (Evans & Johansen 1999). Additionally, lichens serve as shelter to micro-fauna, and as food sources to animals, including large antelope (Wessels *et al.* 1979; Tuba *et al.* 1998). Lichens growing in the soil crust niche are some of the most susceptible lichens to human impacts around the globe, and damage to biological soil crusts has been examined in several arid regions such as the south-west United States, Australia, and the Negev Desert in Israel (Anderson *et al.* 1982; Belnap & Gillette 1998; Bolling & Walker 2000; Eldridge 2000). The recovery rates of biological crusts have been found to be extremely slow, particularly in arid landscapes (Evans & Belnap 1999). Hence, the damage to lichen-covered soil crusts by off-road vehicles in the central Namib has led to mounting concern about the long-term effects on the desert environment (Seely & Hamilton 1978; Wessels & van Vuuren 1986; Daneel 1992).

Until recently, the northern Namib has had far less disturbance than other regions due to its remote location. Before human activities such as open cast mining and extensive off-road driving escalate to a level that may threaten lichen soil crusts in the north, information is required on community composition and distribution of soil crust lichens in this sub-region of the Namib. With this study, we aim to increase our understanding of these lichen communities through a structured survey of the northern Namib Desert, exploring distribution patterns and species richness between isolated communities within the northern Namib and between other sub-regions of the Namib.

Materials and Methods

Study area

The Namib Desert extends from South Africa, through Namibia, and into Angola, covering roughly 2000 km of Africa's south-west coastline (Goudie 2002). Most of the desert falls inside Namibian borders. The Namib is one of the driest deserts in the world, receiving a mean annual rainfall of 19 mm along the coast (Lancaster *et al.* 1984; Seely 1984; Southgate *et al.* 1996; Simmons *et al.* 1998). However, fog moisture is blown inland by the predominant south-west winds between 30 and 200 days in a year (Lancaster *et al.* 1984; Southgate *et al.* 1996). Fog intensity varies considerably along both latitudinal and longitudinal gradients, but mean annual fog precipitation has been estimated to range between 37 mm and 87 mm (Lancaster *et al.* 1984; Olivier 1992; Southgate *et al.* 1996; Hachfield 2000). Similar climatic conditions occur in only two other deserts in the world, the Atacama Desert in Chile, and the Sonoran Desert on the western coast of the United States (Rundel 1978). Although not enough to initiate the germination of plants, regular fog events sustain most life in the Namib, creating an isolated environment conducive to high rates of species diversity and endemism compared with other hyper-arid regions of the world (van Zinderen Bakker 1975; Seely 1978; Southgate *et al.* 1996).

The 3000 km^2 study area falls inside the Skeleton Coast Park of Namibia between the Hoarusib River in the south and the Munutum River in the north (Fig. 1). Habitats in the study area range from coastal plains, to mountains, sand dune fields and gravel plains. Gravel plains harbour soil crust lichens and vary in gravel type, gravel size, and gravel cover. Furthermore, the physical structure of the soil crusts varies according to soil characteristics, namely the presence of calcrete and gypsum (Goudie 1972; Scholz 1972).

Sampling method

The study area was randomly sampled within stratified lichen-rich areas. Stratification took place in February 2002 through the use of aerial photographs from 1974 along with ground truthing, and by using results of lichen surveys from the central Namib (Wessels & van Vuuren 1986; Schieferstein & Loris 1992). Seven habitat sampling areas were identified *a priori* and the boundaries of the these habitat types recorded using a Global Positioning System (GPS) and mapped with ArcView 3.1 geographic information system software (Fig. 1). The common feature of all seven habitats was the presence of surface gravel cover, although this cover varied considerably between habitats, contributing to the variations found in the lichen–substratum interface. Habitats were therefore distinguished according to gravel clast size and other geomorphic features such as physical soil crust type, slope, and distance from major geomorphic features of the area (i.e. large ephemeral rivers or sand dune fields). For sampling purposes, these habitats were also subdivided geographically, as location is likely to determine unmeasured environmental characteristics such as the accumulation of fog, wind direction, wind intensity, dust accumulation, and temperature. The geographical distinction within habitat types produced a total of 12 sampling sites (Table 1).

The 12 sampling sites were divided into a grid, each subdivision measuring 1 km × 1 km, and 10% of the resulting quadrats were selected for sampling. Off-road driving was ruled out due to the resulting damage to fragile soil crusts, so all sampling was carried out on foot. For this reason, only quadrats within four kilometres of a road were considered for sampling. Within each 1 km × 1 km quadrat, five 10 m × 10 m sub-quadrats were sampled along a line transect running west to east following Will-Wolf *et al.* (2002). If a line transect followed a geomorphic feature different from the overall habitat type, such as an ephemeral stream channel or linear dune ridge, then a different line transect was chosen moving north to south through the quadrat. The 10 m × 10 m sub-quadrats were sampled by first recording altitude, slope direction, and general geomorphic features. Then the structural–physiognomic characteristics of the vegetation were

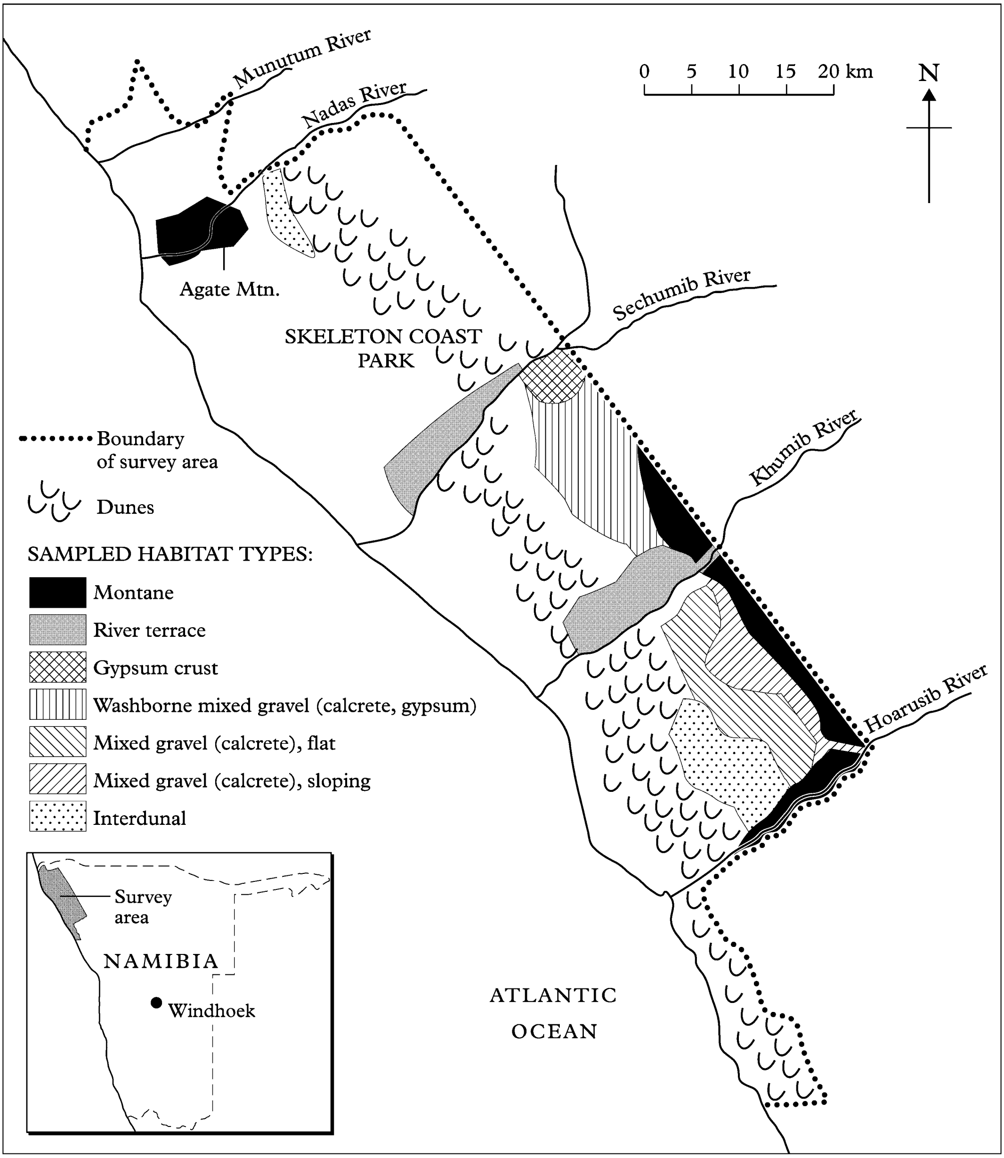

FIG. 1. Map of study area in the northern Namib Desert of Namibia showing the boundaries of each of the seven lichen habitat types.

recorded, i.e. grass or shrub, following Werger and Sprangers (1982). Higher plants are rare on lichen-rich gravel plains of the Namib, so here vegetation data were used only to characterize the habitats on a landscape scale. Sampling took place between January and March 2001 during the rainy season, so that annuals could be located.

Within a smaller 0·5 m × 0·5 m plot, lichen cover, gravel clast size, and soil crust thickness were recorded. Such nested sampling methods of lichen cover have been successfully used in previous studies where lichen distribution patterns and species lists were unknown (McCune & Lesica 1992). The 0·5 m × 0·5 m lichen sampling plot was chosen by visually determining the point with the most diverse lichen cover. This method reduced the chance of missing a special lichen niche, and also helped to identify lichen hotspots within the study area following Neitlich and McCune (1997). The sampling of lichens consisted of initial morphological classification of all species and identification of

TABLE 1. *Seven lichen soil crust habitats in the northern Namib Desert and their subdivided sampling sites described according to total area, geomorphic features, and vegetation*

Habitat type	Area (km^2)	Geomorphic features	Vegetation (*rarely present)
1. Mixed gravel plain w/calcrete (E of dunes)	110	E of dunefield; flat with undulating sediment deposits; average gravel size ≤10 mm; physical soil crust thickness ≤10 mm.	Seasonal grass, succulents*
2. Mixed gravel w/calcrete, sloping	43	W of mountain ridge; ephemeral stream channels; W facing slope; average gravel size ≤10 mm; average physical soil crust thickness ≤10 mm.	Seasonal grass, succulents*
3. Interdunal			
A. South	44	Bordering linear dunefield—barchan and gravel dunes; granite outcrops; average gravel size ≤10 mm; physical soil crusts absent.	Succulents*
B. North	38	Flat with vegetated dunes; average gravel size ≤10 mm; physical soil crusts absent.	Succulents*, shrubs*
4. River terraces			
A. Khumib River	46	River terraces; S–SW facing slope; mixture of lithologies; mixed gravel; physical soil crust thickness ≤10 mm.	Seasonal grass*
B. Sechumib River	54	River terraces; S & W facing slope; mixed gravel; physical soil crust thickness ≤10mm.	Seasonal grass*
5. Montane			
A. North Khumib	50	Terraces (pediment and washborne sediment); open plains; granite outcrops; ephemeral stream channels; W, E, N, S facing slopes; mixed gravel; physical soil crusts ranged from ≤10 mm on plateaus to >10 mm on hillsides.	Seasonal grass, succulents*, shrubs*
B. South Khumib	82	Terraces (pediment and washborne sediment); open plains; granite outcrops; ephemeral stream channels; W, E, N, S facing slopes; mixed gravel on plateaus and large fraction, >10mm, on hillsides; physical soil crusts ranged from ≤10 mm on plateaus, to >10 mm on hill tops.	Seasonal grass, succulents*, shrubs*
C. Agate Mountain	40	Terraces (pediment and washborne sediment); open plains; granite outcrops; ephemeral stream channels; steep W, E, N, S facing slopes; mixed gravel; physical soil crusts ranged from ≤10 mm on plateaus, to >10 mm on hillsides.	Seasonal grass*, succulents*
D. Hoarusib River N	43	Terraces (pediment and washborne sediment); open plains; granite outcrops; ephemeral stream channels; W, E, N, S facing slopes; mixed gravel; physical soil crusts were either absent, or ranged from ≤10 mm on plateaus, to >10 mm on hillsides.	Seasonal grass*, succulents*
6. Washborne mixed gravel w/calcrete and gypsum	100	River terraces; rounded mixed gravel; broad ephemeral river channel with loose alluvial sediment between low mt. ranges; E & W facing slopes; mixed gravel; physical soil crust thickness >10mm.	Seasonal grass, succulents*, shrubs*
7. Gypsum crust	38	River terraces; S of broad ephemeral river; E of dunes; W of low mt. range; mixed gravel; physical soil crusts >10 mm.	Seasonal grass*, succulents*, shrubs, trees*

individual lichen species where possible. Chemical tests were used in the field to differentiate between species that looked similar, using calcium hypochlorite and potassium hydroxide. Unknown species were collected for later identification. The percentage of lichen cover in the 0·5 m × 0·5 m quadrat was recorded, as well as the cover and largest diameter of the dominant species. For fruticose species, both the diameter and height were measured and the larger of the two was recorded.

Average gravel clast sizes were recorded by measuring the largest and smallest gravel clasts in the 0·5 m × 0·5 m sampling plots, limiting measurements to stones between 2 mm and 250 mm diameter, following geological scales of gravel, pebble, and cobble sizes (Greensmith 1978). Measurements fell into three categories for the purpose of this study: ≤10 mm if both measurements fell below 10 mm; >10 mm if both measurements fell above 10 mm; and mixed if each measurement fell on either side of 10 mm. Physical soil crust types were categorized by the thickness of the crust, not including any surface biological growth. Thickness was ranked into three categories based on measurements in each of the 12 sites and on previous soil crust studies: sandy (no crust); thin crust (≤10 mm); and thick crust (>10 mm) (Graef & Stahr 2000). The presence of cyanobacteria and algae contribute to the physical structure of crusts, including thickness, but for the purpose of this study there was no separate assessment of these components.

Data analysis

Prior to data analysis, minimum sampling efforts were calculated for each sampling site using a species accumulation curve in Species Diversity and Richness software 2.6, ensuring that sampling efforts were sufficient in all sampling sites (Henderson & Seaby 2001). Lichen species presence and absence in the 12 sampling sites were compared using the Jaccard similarity coefficient in SPSS 11.5 (Kent & Coker 1992; Kinnear & Gray 2000).

Each sampled lichen community was analyzed for species richness, referred to here as the total number of lichen species found in the 0·5 m × 0·5 m sampling plots (Magurran 1988). Lichen species richness in a soil crust community can be indicative of the developmental level of the biological soil crust, with higher species counts usually indicating a well-developed crust due to the slow establishment and growth of lichens (Ponzetti & McCune 2001; Evans & Johansen 1999). However, in some cases a community becomes mono-specific in later stages of development due to competitive exclusion (Lawrey 1991). Therefore, records of lichen cover in the 0·5 m × 0·5 m plots and the largest size of the communities' dominant lichen species were also assessed.

A lichen community development index was created using the three values of species richness, cover, and size, which was used to determine variations in the developmental level of the lichen soil crust communities across the 12 sites and seven habitat types. These values were transformed as a percentage of a lichen community optimum. The largest value found in the 12 sites for each category was used as the lichen community optimum, against which other site communities were scaled. The data transformation normalized the subdata set and also prevented large values from skewing the overall index when all three categories were added up to the final index score. The added values fell along a scale of zero to three, with zero being the least developed lichen soil crust community and three being the most highly developed lichen soil crust community.

Distribution patterns of lichens were examined using a subset of samples that excluded sites with zero lichen cover and sites where environmental data were incomplete. Relationships between species and environmental data were analysed using canonical correspondence analysis (CCA) in CANOCO 4.5 and Spearman's rank correlation in SPSS 11.5 (ter Braak 1988; Kinnear & Gray 2000). CCA ordinates species and sites using correspondence analysis, and simultaneously uses multiple regression on the associated environmental variables to guide the final ordinating according to the relationships between the environmental variables and the species data. The output is useful in generating hypotheses about relationships between environmental variables and the structure of a biological community. Here it is used to interpret the species variance found in the study area across the 12 sites. Highly correlated environmental variables were removed before the CCA was run, leaving five environmental variables. In addition, Spearman's rank correlation was used to identify correlations between the five environmental variables used in the CCA, and the three lichen community characteristics used in the community development analysis: species richness, largest lichen size, and lichen cover.

Results

Lichen species

A total of twenty-eight lichen species were found in the soil crust communities sampled in the northern Namib Desert (Table 2). Of these twenty-eight species, thirteen were found as the dominant species in a community. The number of species found in this survey is similar to that found in the central and southern Namib, but overall species lists differed between the regions (Schieferstein & Loris 1992; Jurgens & Niebel-Lohmann 1995). The most dominant species, such as *Caloplaca elegantissima* and *Xanthoparmelia walteri*, were common across all three regions. Other species found in this survey that were also relatively common in one or both of the other regions of the Namib were:

TABLE 2. *Terricolous lichen species recorded in the northern Namib Desert, and the habitats and sampling sites where they occurred*

	Morphological group*	Substratum	Sites†											
			1	2	3.1	3.2	4.1	4.2	5.1	5.2	5.3	5.4	6	7
Acarospora negligens H. Magn. [Doidge 1950]	Crst	Gr								X		X		
A. schleicheri A. Massal. [Almborn 1988]	Crst	Gr, soil											X	X
Buellia sp. 1	Crst	Gr, soil											X	X
Buellia sp. 2	Crst	Gr						D			X		D	X
Buellia sp. 3	Crst	Gr, soil	X		X			X	D				X	
Caloplaca elegantissima Zahlbr. [Poelt & Pelleter 1984]	Crst	Gr	D	X	X	D	D	D	D	D	X	X	D	D
C. eudoxa Zahlbr. [Poelt & Pelleter 1984]	Sfrut	gr, vag	D		D									
C. isidiosa Kärnefelt (1988*a*)	Crst	gr, soil	X				X						X	X
C. namibensis Kärnefelt (1988*b*)	Crst	gr, soil	D	X	D	X	D	D	X	D	X	X	D	X
C. volkii Wirth & Vězda (1975)	Crst	gr, soil											X	X
Endolithic	Crst	gr	X											
Lecanora sp.	Crst	gr, soil		X	X				X	X			X	X
Lecidella crystallina Wirth & Vězda (1975)	Crst	gr, soil		X				X	X			X	D	X
Neofuscelia namibiensis Elix (1999)	Fol	gr	D	X	X		X	D	D	D		X	D	X
Parmelia sp. green	Fol	gr, svag	X											
Parmelia sp. white	Frut	vag	X		D									
Ramalina capensis (Nyl.) Zahlbr.	Frut	gr									X			
Ramalina sp.	Frut	gr							X	X	X	X	X	X
Santessonia hereroensis (Vain.) Follmann (1987)	Frut	gr							X	X	X			X
S. namibensis Sérusiaux & Wessels (1984)	Frut	gr, vag	X		X				X	X				X
Teloschistes capensis (L.f.) Müll.Arg. [Almborn 1989]	Frut	gr		X					D	D	D		D	X
Usnea sp.	Frut	gr											X	X
Xanthomaculina convoluta Hale (1985)	Fol	vag	D		X		X						X	
X. hottentotta Hale (1985)	Fol	gr							X	X	D	X		X
Xanthoparmelia harissii Hale (1989)	Fol	gr								X				
X. serusiauxii Hale (1986)	Fol	gr							X	X		X	X	X
X. walteri M.D.E. Knox (1983)	Fol	gr	D	D	X		D	D	D	D	D	D	D	D
Xanthoria flammea Hillman (1922)	Frut	vag							D			D		
Total number of sampling sites			55	20	20	10	20	25	20	35	15	10	50	20
Minimum sampling effort (sp. accumulation curve)			34	5	10	5	5	12	14	11	3	7	12	16

*crst=crustose; fol=foliose; frut=fruticose; sfrut=subfruticose; gr=gravel; vag=vagrant; svag=subvagrant.

†X=present in site; D=dominant species in one or more sample plots within site; 1=mixed gravel with calcrete; 2=mixed gravel with calcrete, sloping; 3.1=interdunal, south; 3.2=interdunal, north; 4.1=river terrace, Khumib; 4.2=river terrace, Sechumib; 5.1=montane, N. Khumib; 5.2=montane, S. Khumib; 5.3=montane, Agate; 5.4=montane, Hoarusib; 6=washborne gravel with calcrete and gypsum; 7=gypsum crust.

Lecidella crystallina, *Caloplaca namibensis*, *C. volkii*, *Neofuscelia namibensis*, *Xanthomaculina hottentotta*, *Teloschistes capensis*, and *Xanthoparmelia serusiauxii*.

Despite similarities in the distribution of the common species, there were apparent differences in the presence of certain species between the regions. It was not possible to quantify dissimilarities between the three regions, as species lists for the central and southern Namib do not differentiate between lichens from terricolous, epiphytic and saxicolous niches (Schieferstein & Loris 1992; Jurgens & Niebel-Lohmann 1995). Nevertheless, there were several species found in the northern Namib, such as two unclassified *Parmelia* spp. (one vagrant and one subvagrant), *Caloplaca isidiosa*, *Xanthoparmelia harrisii*, and an *Usnea* sp. that have not been recorded on lists for the other two regions of the Namib. There were also several species in the northern Namib that demonstrated vagrant growth forms that have not been recorded in the other regions of the Namib.

Two vagrant species were found in the study area, a new undescribed *Parmelia* sp., and the common *Xanthomaculina convoluta*. In addition, several lichen species that are normally substratum-dependent, were found in vagrant to sub-vagrant forms in the study area. The endemic sub-fruticose species *Caloplaca eudoxa* was dominant in isolated interdunal sites where it grew completely unattached or attached only to minute stones, enabling it to wind disperse. The less dominant *Neofuscelia namibensis*, a second undescribed *Parmelia* sp., and the crustose species *Caloplaca elegantissima* and *Lecidella crystallina* also demonstrated this same variation in growth form. These growth forms were recorded primarily along the boundary between the mixed gravel plain with calcrete habitat (site 1) and the interdunal habitat (site 3.1). A common Namib Desert epiphytic species, *Xanthoria flammea*, was also found growing in a vagrant form in isolated, dense, mono-specific communities within the montane habitat. None of these vagrant forms have been recorded in the central and southern Namib.

Species composition also varied across the 12 sample sites in the northern Namib. When the sites were compared using the Jaccard similarity coefficient, S_j values fell below the commonly used threshold of 0·9 for all paired sites. The values of S_j range between zero and one, with one denoting complete similarity and zero denoting no similarity. Values were as high as 0·714 between the montane sites. The two most dissimilar sites were interdunal, north (site 3.2) and gypsum crust (site 7) (S_j=0·111).

Morphological groups

The most widespread morphological group in the northern Namib was the crustose group, which included the most common genus in the study area *Caloplaca*, with *C. elegantissima* and *C. namibensis* occurring in all habitats (Table 2). The foliose group was the second most widespread morphological group with *Xanthoparmelia walteri* being the most frequently recorded foliose lichen in the study area. The most common fruticose lichen recorded in the study area was *Teloschistes capensis*.

Crustose species were not only the most widely distributed morphological group in this study, but were also the most diverse and showed growth adaptations. For example, specimens of *Caloplaca elegantissima* and *C. namibensis*, which occurred across all habitats, were often found with thallus margins upturned to optimize fog absorption. *Lecidella crystallina* was found in a free-growing, bunched form that may also be more conducive to fog absorption than when growing fully adnate to the substratum.

Common foliose species, such as the widespread *Xanthoparmelia walteri*, had similar distribution patterns in all three regions of the Namib. Lichen cover in foliose-dominated communities in the northern Namib was frequently dense, but often with a low diversity of species. Vagrant foliose communities showed greater species richness, a feature which has not been recorded in other regions of the Namib.

TABLE 3. *Lichen community development index*. Three variables of lichen communities are listed for each of the 12 sampling sites*

	Species richness		Lichen cover (% in 0·5 × 0·5 m plots)		Mean largest size of dominant species (mm)		Lichen community development index (sum of transformed values on a scale of 0–3)
Habitat	Value	% of max. (18)	Value	% of max. (71·7)	Value	% of max. (79·9)	
1	12	0·67	20·6	0·29	39·6	0·50	1·45
2	7	0·39	64·3	0·90	79·9	1·00	2·29
3.1	10	0·56	30·9	0·43	13·3	0·17	1·15
3.2	2	0·11	9·2	0·13	27·8	0·35	0·59
4.1	6	0·33	15·8	0·22	40·3	0·50	1·06
4.2	7	0·39	9·4	0·13	48·0	0·60	1·12
5.1	14	0·78	19·5	0·27	46·2	0·58	1·63
5.2	13	0·72	32·2	0·45	64·2	0·80	1·97
5.3	9	0·50	12·7	0·18	40·5	0·51	1·18
5.4	10	0·56	25·9	0·36	47·1	0·59	1·51
6	17	0·94	16·4	0·23	51·0	0·64	1·81
7	18	1·00	71·7	1·00	72·1	0·90	2·90

*Values for each site represent the percentage (in decimal form) of the maximum value found for that category in the sampled population. The sum of these transformed values are used as indicators of lichen soil crust community development on a scale of zero to three. Zero denotes the lowest community development on the scale, and three denotes the highest.

Fruticose species were found less frequently than expected, considering the large and dense fruticose communities occurring in the central and southern Namib. *Teloschistes capensis* was the most common fruticose species, as in the other regions, but was restricted to small patches in montane sites and as sparsely distributed components of foliose-dominated communities (sites 2, 6, & 7).

Lichen community development index

Species richness was highest in the gypsum crust site habitat (site 7) and lowest in the interdunal habitat (site 3.2) (Table 3). The highest percentage of lichen cover in the study area was found in plots within the gypsum crust habitat (site 7), the montane habitat (sites 5.1–5.4), as well as mixed gravel with calcrete–sloped (site 2), a habitat with low species richness (Table 3). The largest lichen thalli found in the study area were also found in the three most species rich sites, in addition to the more mono-specific site 2.

Values for the lichen community development index for each of the 12 sites are given in Table 3. The maximum values used as the basis for data transformations were found in the gypsum crust habitat (site 7) for the categories of species richness and percentage of lichen cover. But the largest, optimum lichen size was found in the mixed gravel with calcrete–sloped habitat (site 2). The sum of the transformed values fell within a range of zero to three, with three denoting the highest level of community development and zero denoting the lowest. The highest index score out of all 12 sites was 2·9 in the gypsum crust habitat (site 7), and the lowest score was found in the interdunal–north habitat (site 3.2). Mixed gravel with calcrete–sloped (site 2) had the second highest score, despite the mono-specific nature of lichen communities in this habitat.

Lichen distribution

The CCA ordination illustrates that gravel clast size was the most important

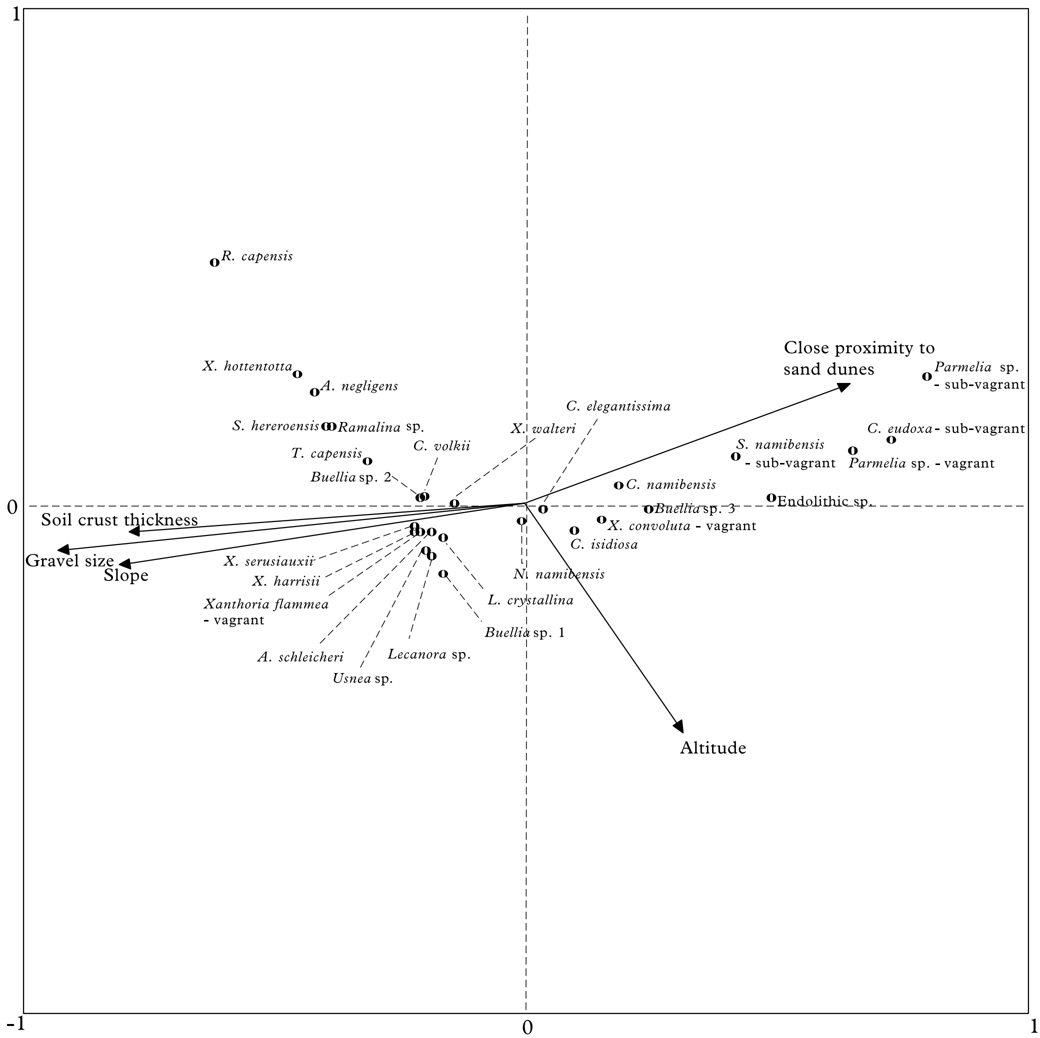

FIG. 2. Canonical correspondence analysis species—environment biplot for axes 1 and 2, illustrating the variance in species distribution, constrained by five environmental variables. The two axes combined explain 74·6% of the variance. The first axis explains 48·8% of the variance, Eigenvalue = 0·39. On axis 1, gravel clast size accounts for the majority of variance with eigenvalue of − 0·8948. Next is slope (− 0·84), soil crust thickness (− 0·74), proximity to sand dunes (0·62), and altitude (0·23).

determinant of lichen species variation across the 12 sites, followed by slope, soil crust thickness, proximity to sand dunes, and altitude (Fig. 2). The Spearman's rank correlation values between these five variables and lichen species richness, cover, and size are given in Table 4. The environmental variable showing the highest correlations with the three lichen community characteristics was soil crust thickness. A consistently significant correlation ($P<0{\cdot}05$) also occurred with gravel clast size. Correlations with the other three environmental variables were inconsistent, with significant correlations occurring with only one or two of the lichen community characteristics.

TABLE 4. *Spearman's rank correlation values between five environmental variables and the three lichen community characteristics of lichen species richness, cover, and size*

	Lichen spp. richness		Lichen cover		Largest lichen size	
$n=100$	r_s	p	r_s	p	r_s	p
Gravel clast size	− 0·221	<0·05	− 0·252	<0·05	0·327	<0·01
Soil crust thickness	0·286	<0·01	0·253	<0·05	0·418	<0·01
Altitude	0·192	>0·05	0·342	<0·01	0·114	>0·05
Slope	0·224	<0·05	− 0·208	<0·05	0·072	>0·05
Dune proximity	− 0·096	>0·05	0·114	<0·05	− 0·407	<0·01

Discussion

Lichen species and morphology

Crustose species in the terricolous niche have a wide distribution in the northern Namib, which differs from their distributions recorded in the central and southern regions of the Namib and those found in other fog deserts (Rundel 1982, Redon 1982). Schieferstein & Loris (1992) described an extensive, continuous crustose-dominated lichen field in the central Namib, but none are described in the southern Namib. In deserts where terricolous crustose lichens are common, cyanolichens usually dominate with a high correlation to rainfall patterns (Eldridge 1996; Lange *et al.* 1998). In the Namib Desert where rainfall is infrequent, chlorolichens dominate and are more successful at utilizing water vapour than cyanolichens (Rundel 1978). But despite their better use of water vapour, chlorolichens of the crustose group still show a tendency to grow in water run-off areas in fog deserts (Rundel 1982; Redon 1982). Although crustose lichens in the northern Namib were found on a wide range of epigeic substrata, they showed preferences for large gravel stones and soil surfaces roughened by gypsum or calcrete. These substrata may provide enough water run off for the development of crustose communities when thallus adaptations for water capture alone are insufficient.

Foliose and fruticose lichens are known to be more efficient at absorbing atmospheric moisture, which is supported by the widespread occurrence of foliose species in this survey (Rundel 1978, 1982; Nash *et al.* 1979, 1982). The most obvious variation in foliose species between the three regions of the Namib was the presence of several vagrant and sub-vagrant species. Wind dispersal of thalli is used by vagrant species in semi-arid to arid regions where vegetation is scarce (Eldridge & Leys 1999). The more frequent occurrence of sub-vagrant and vagrant species in the northern Namib proves that variations occur between lichen soil crust habitat types in the three different regions of the Namib Desert.

The optimal fog-absorbing morphology of fruticose species is well illustrated in the central and southern Namib, where dense communities of *Teloschistes capensis* and *Ramalina capensis* dominate gravel plains along the coast (Schieferstein & Loris 1992; Jurgens & Niebel-Lohmann 1995). However, fruticose species were the least widespread morphological group in the northern Namib, which may be due to a lack of suitable habitat directly along the coastline. The northern Namib has extensive saltpans along the coast, and most lichen-rich gravel plains are between 10 km and 30 km inland. Inland geomorphology also differs from that found in other regions of the Namib, possibly contributing to variations in fog deposition. According to Olivier (1992) fog density and frequency in the three different regions of the Namib differ. The significant differences found in fruticose species distributions warrant further investigation into variables such as fog deposition, which may explain much of the variance in lichen community compositions in the Namib

Desert. A greater understanding of soil crust lichen distribution patterns may add weight to suggestions that the Namib is made up of three different biomes (Walter 1986).

Local variations in lichen communities are also apparent within each of the regions. The variance found within the northern Namib Desert was substantiated not only by the low Jaccard similarity coefficients found between paired sites, but also by the lichen community development index. Index scores illustrate the range of terricolous lichen community types occurring in the northern Namib, based on the development of the communities. Index scores of this kind can help to quantify differences between lichen soil crust types for ecological purposes and also for use in biome descriptions and conservation planning in the three different regions.

Lichen distribution within the northern Namib

Habitat descriptors were investigated in this study for correlations with lichen distribution patterns, to help further understand lichen soil crusts and soil crust habitat types in the Namib Desert. The results of the CCA and the Spearman rank correlations showed that gravel clast size and soil crust thickness were the closest links to the distribution patterns of terricolous lichens in the northern Namib (Figure 2; Table 4). In the CCA biplot, slope also proved to be significantly related to lichen distribution.

Both gravel size and soil crust thickness contribute to the stability of the physical soil crust. Much has been written on the relationship between soil crust stability and lichen growth, and there appears to be a consistent correlation between the two (Eldridge & Tozer 1997; Eldridge & Koen 1998). While established lichen communities contribute to the stability of the soil crust, the physical soil crusts allow soil-bound species to develop (Garcia-Pichel & Belnap 2001). Gravel cover generally stabilizes sandy soil and contributes to the micro-topography, thus increasing the surface area available for lichen growth and providing micro-relief where lichen fragments can collect. Soil crust thickness varies between wind crusts, rain crusts, calcrete, clay, and gypsum crusts, and the thickness of the crust is usually indicative of the stability of the soil substratum (Eldridge & Tozer 1997; Eldridge & Leys 2003). Gypsum increases the soil crust thickness and micro-relief, and is known to harbour well-developed biological soil crusts and high species richness, as seen in this study and others (St. Clair *et al.* 1993).

There are several other micro-environmental variables that may dictate lichen distribution, which were not assessed in this study. Given the patchy, mosaic cover in many of the habitats in the Namib Desert, there are certainly micro-environmental dimensions on which distribution patterns are based. These may include chemical characteristics of soil, such as salinity or pH as found in other studies (Eldridge & Tozer 1997; Ponzetti & McCune 2001). The presence of other biotic components in the soil, such as cyanobacteria, could also be related to the incidence of lichen growth (Garcia-Pichel & Belnap 1996).

On a macro-scale, the CCA ordination in this study showed a relationship between lichen species distribution and the variables of slope, dune proximity, and altitude (Fig. 2). Slope, along with altitude and elevation has been influential in lichen patterning in other studies, and here they may be closely correlated with fog exposure and therefore lichen distribution (Redon 1982; Pirintsos *et al.* 1995). Slopes facing the predominant fog-bearing winds in the Namib have been associated with foliose and fruticose species in the study by Schieferstein & Loris (1992). Fog exposure has also been linked to the presence of gypsum in Namib Desert soils, which provides greater micro-relief in gravel plains and may dictate water run-off and the potential infiltration of the soil (Eckardt & Spiro 1999).

Moisture availability is the most common link to lichen distribution patterns in deserts (Nash *et al.* 1979; Eldridge 1996; Eldridge &

Koen 1998; Lange *et al.* 1998). Nash *et al.* (1979) studied lichens in the fog belt of Baja California and demonstrated a significant correlation between lichen community compositions and fog availability. Schieferstein and Loris (1992) recorded similar results in the central Namib, where three fog zones based on distance from the coast were correlated with lichen cover. Variations in geomorphology along the Namibian coastline most probably dictate the dispersal of fog, so that zones identified in the central Namib may not occur in the northern Namib, as suggested by lichen distribution patterns found in this study.

Schieferstein & Loris (1992) also concluded that exposure to east winds had a negative effect on lichen cover, due mainly to the large deposits of aeolian dust during east wind storms. This study found that certain species tolerated dust and close proximity to sand dunes, but there were still negative relationships between dune proximity and most lichen species in the area (Fig. 2). In all of the vagrant species habitats sampled in this study, dust exposure is persistent, so there are clearly several species and growth forms that are able to tolerate wind and dust. Schieferstein & Loris (1992) found that there was a total absence of lichen growth to the west of large sand dune systems, and the same was found in the northern Namib. However, in light of the number of wind-dispersed and dune-tolerant species found in this survey, the total absence of lichens may be better explained by the lack of contiguous lichen habitat from where lichen fragments and spores could migrate.

Wind may also be a key variable dictating the distribution patterns of terricolous lichens, as suggested by the sub-vagrant and vagrant species found in the northern Namib Desert. Vagrant species were found in the mixed gravel with calcrete (site 1), interdunal (site 3.1 and 3.2) and montane habitat types (sites 5.1 and 5.4); all wind-exposed areas. The other common characteristic in the habitats of vagrant species was the presence of loose sandy soil sediments with a sparse, small gravel cover. This substratum is less likely to support dense grass growth in years of annual rainfall, which could impede movement of these wind-dispersed species, as would larger gravel clasts. Again, these combined local and landcape variables require investigation before we can understand the dimensions controlling lichen community distributions between and within the three regions of the Namib Desert.

Conclusion

Lichen community composition and distribution patterns appear to vary between the northern, central, and southern Namib, indicating that inter-regional differences may be significant enough to require separate consideration in ecological assessments of the Namib Desert. Such variations may further support suggestions that the Namib encompasses three distinct biomes. Identifications are still required for several of the species found during this survey, and species lists and distribution patterns require further investigation in all regions of the Namib before accurate comparisons can be made.

Recognizing differences in terricolous lichen communities across the Namib Desert is not only of ecological interest, but would also have significant implications for land-use planning. Results of this study also suggest a need to make distinctions between habitat types, as soil crust communities varied considerably across the northern Namib. Lichen community development indices could guide zonation of fragile lichen soil crust areas for management purposes, if combined with environmental variables in each habitat. The non-linear and often mosaic distribution patterns found in this survey indicate that lichen cover in the Namib is most probably dictated by many of the same variables identified in other arid regions, but much work is needed to confirm the identity of the most significant environmental variables in this unique fog desert. A well-researched index that considers all significant variations in macro- and micro-environments of the Namib, could also help determine the recovery rates of lichen soil crusts. Recovery assessments are urgently needed, particularly in the central Namib where extensive disturbance has already taken place. At present, our understanding of lichen soil crusts in the Namib Desert is not adequate enough to confidently address conservation issues surrounding these important primary producers. Terricolous lichen surveys in the remote and understudied regions of this desert are only a first step towards improving our understanding of these fragile components of the Namib Desert.

The Namibia Ministry of Environment and Tourism and the University of Oxford encouraged and supported this project. Project funds were contributed by The Biodiversity Taskforce of Namibia, Wilderness Safaris Namibia and the Wilderness Trust, The Explorers Club of New York, and the Sindisa Foundation. The authors thank Patricia A. Wolseley, Simone Louwhoff, Luciana Zedda, Jack Elix, Emmanuël Sérusiaux, Ingvar Kärnefelt, and Vanessa Winchester who assisted in the identification of lichen species. In Namibia, Joh Henschel advised in the field, and the following field assistants helped with sampling: Dave van Smeerdijk, Tammie Matson, Victoria Cooper, and James Watson who also commented on this manuscript. Additional comments were given by Robert J. Whittaker, who also assisted with the data analysis. Ailsa Allen assisted with the survey area map.

References

Almborn, O. (1988) Some distribution patterns in the lichen flora of South Africa. *Monographs in Systematic Botany from the Missouri Botanical Garden* **25:** 429–432.

Almborn, O. (1989) Revision of the lichen genus *Teloschistes* in central and southern Africa. *Nordic Journal of Botany* **8:** 521–537.

Anderson, D. C., Harper, K. T. & Rushforth, S. R. (1982) Recovery of cryptogamic soil crusts from grazing on Utah winter ranges. *Journal of Range Management* **35:** 355–359.

Belnap, J. & Gillette, D. A. (1998) Vulnerability of desert biological soil crusts to wind erosion: the influences of crust development, soil texture, and disturbance. *Journal of Arid Environments* **39:** 133–142.

Bolling, J. D. & Walker, L. R. (2000) Plant and soil recovery along a series of abandoned desert roads. *Journal of Arid Environments* **46:** 1–24.

Campbell, S. E., Seeler, J. S. & Golubic S. (1989) Desert crust formation and soil stabilization. *Arid Soil Research and Rehabilitation* **3:** 217–228.

Daneel, J. L. (1992) The impact of off-road vehicle traffic on the gravel plains of the central Namib Desert, Namibia. Unpublished Masters Thesis, University of Natal, Pietermaritzburg.

Doidge, E. M. (1950) The South African fungi and lichens to the end of 1945. *Bothalia* **5:** 1–1094.

Eckardt, F. D. & Spiro B. (1999) The origin of sulphur in gypsum and dissolved sulphate in the central Namib Desert, Namibia. *Sedimentary Geology* **123:** 255–273.

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. (2000) Ecology and management of biological soil crusts: recent developments and future challenges. *Bryologist* **103:** 742–747.

Eldridge, D. J. & Koen, T. B. (1998) Cover and floristics of microphytic soil crusts in relation to indices of landscape health. *Plant Ecology* **137:** 101–114.

Eldridge, D. J. & Leys, J. F. (1999) Wind dispersal of the vagrant lichen *Chondropsis semiviridis* in semi-arid Eastern Australia. *Australian Journal of Botany* **47:** 157–164.

Eldridge, D. J. & Leys, J. F. (2003) Exploring some relationships between biological soil crust, soil aggregation and wind erosion. *Journal of Arid Environments* **53:** 457–466.

Eldridge, D. J. & Tozer, M. E. (1997) Environmental factors relating to the distribution of terricolous bryophytes and lichens in semi-arid eastern Australia. *Bryologist* **100:** 28–39.

Elix, J.A. (1999) New Species of *Neofuscelia* (lichenized *Ascomycotina, Parmeliaceae*) from the southern hemisphere. *Mycotaxon* 71: 431–456.

Evans, R. D. & Belnap, J. (1999) Long-term consequences of disturbance on nitrogen dynamics in an arid ecosystem. *Ecology* **80:** 150–160.

Evans, R. D. & Johansen, J. R. (1999) Microbiotic crusts and ecosystem processes. *Critical Reviews in Plant Sciences* **18:** 183–225.

Follmann, G. (1987) Vorarbeiten zu einer Monographie der Flechtenfamilie Roccellaceae Chev. VIII. Inhaltsstoffe und Verwandtschaftsverhaltnese von *Roccella hereroensis* Vain. und *Roccella mossamedana* Vain. *Journal of Plant Physiology* **131:** 145–151.

Garcia-Pichel, F. & Belnap, J. (1996) Microenvironments and microscale productivity of cyanobacterial desert crusts. *Journal of Phycology* **32:** 774–782.

Garcia-Pichel, F. & Belnap, J. (2001) Small-scale environments and distribution of biological soil crusts. In *Biological Soil Crusts: Structure, Function, and Management* (J. Belnap and O. L. Lange, eds): 193–213. Berlin: Springer-Verlag.

Goudie, A. (1972) Climate, weathering, crust formation, dunes, and fluvial features of the central Namib Desert, near Gobabeb, South West Africa. *Madoqua* **2:** 15–31.

Goudie, A. (2002) *Great Warm Deserts of the World: Landscapes and Evolution*. New York: Oxford University Press.

Graef, F. & Stahr, K. (2000) Incidence of soil surface crust types in semi-arid Niger. *Soil and Tillage Research* **55:** 213–218.

Greensmith, J. T. 1978. *Petrology of the Sedimentary Rocks*. Surrey: George Allen & Unwin.

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.

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

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

Hale, M. E. (1989) New species in the lichen genus *Xanthoparmelia* (Ascomycotina: *Parmeliaceae*). *Mycotaxon* **34:** 541–564.

Henderson, P. A. & Seaby, R. M. H. (2001) *Species Diversity and Richness Version 2.65*. Lymington: Pisces Conservation.

Hill, M. O. (1979). *TWINSPAN—a FORTRAN Program for Arranging Multivariate Data in an Ordered Two-Way Table by Classification of the Individuals and Attributes*. Ithaca: Cornell University.

Hillmann, J. (1922) Übersicht über die Arten der Flechten-Gattung *Xanthoria* (Th. Fr.) Arn. *Hedwigia* **63:** 198–208.

Jurgens, N. & Niebel-Lohmann, A. (1995) Geobotanical observations on lichen fields of the Southern Namib Desert. *Mitteilungen aus dem Institut für Allgemeine Botanik Hamburg* **25:** 135–156.

Kärnefelt, I. (1988*a*) Morphology and biogeography of saxicolous *Caloplaca* in Southern Africa. *Monographs in Systematic Botany from the Missouri Botanical Garden* **25:** 439–452.

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

Kent, M. & Coker, P. (1992) *Vegetation Description and Analysis—A Practical Approach*. London: Belhaven Press.

Kinnear, P. R. & Gray, C. D. (2000) *SPSS for Windows Made Simple*. East Sussex: Psychology Press.

Knox, M. D. E. (1983) New *Xanthoparmeliae* (Lichenes) from southern and central Africa. *Journal of Southern African Botany* **49:** 143–159.

Lancaster, J., Lancaster, N. & Seely, M. K. (1984) Climate of the central Namib Desert. *Madoqua* **14:** 5–61.

Lange, O. L., Belnap, J. & Reichenberger, H. (1998) Photosynthesis of the cyanobacterial soil-crust lichen *Collema tenax* from arid lands in southern Utah, USA: role of water content on light and temperature responses of CO_2 exchange. *Functional Ecology* **12:** 195–202.

Lawrey, J. D. (1991) Biotic interactions in lichen community development: a review. *Lichenologist* **23:** 205–214.

Magurran, A. E. (1988) *Ecological Diversity and its Measurement*. London: Chapman and Hall.

McCune, B. & Lesica, P. (1992) The trade-off between species capture and quantitative accuracy in ecological inventory of lichens and bryophytes in forests in Montana. *Bryologist* **95:** 296–304.

Nash III, T. H., Nebeker, G. T., Moser, T. J. & Reeves, T. (1979) Lichen vegetational gradients in relation to the Pacific Coast of Baja California: the maritime influence. *Madrono* **26:** 149–163.

Nash, T. H., Moser, T. J., Bertke, C. C., Link, S. O., Sigal, L. L., White, S. L. & Fox, C. A. (1982) Photosynthetic patterns of Sonoran Desert lichens. I. Environmental considerations and preliminary field measurements. *Flora* **172:** 335–345.

Neitlich, P. N. & McCune, B. (1997) Hotspots of epiphytic lichen diversity in two young managed forests. *Conservation Biology* **11:** 172–182.

Olivier, J. (1992) Some spatial and temporal aspects of fog in the Namib. *South African Geographer* **19:** 106–126.

Pirintsos, S. A., Diamantopoulos, J. & Stamou, G. P. (1995) Analysis of the distribution of epiphytic lichens within homogeneous *Fagus sylvatica* stands along an altitudinal gradient (Mount Olympos, Greece). *Vegetatio* **116:** 33–40.

Poelt, J. & Pelleter, U. (1984) Zwergstrauchige arten der flechtengattung *Caloplaca*. *Plant Systematics and Evolution* **148:** 51–88.

Ponzetti, J. M. & McCune, B. P. (2001) Biotic soil crusts of Oregon's shrub steppe: community composition in relation to soil chemistry, climate, and livestock activity. *Bryologist* **104:** 212–225.

Redon, J. (1982) Lichens of arid South America. *Journal of the Hattori Botanical Laboratory* **53:** 337–339.

Rundel, P. W. (1978) Ecological relationships of desert fog zone lichens. *Bryologist* **81:** 277–293.

Rundel, P. W. (1982) The role of morphology in the water relations of desert lichens. *Journal of the Hattori Botanical Laboratory* **53:** 315–320.

Schieferstein, B. & Loris, K. (1992) Ecological investigations on lichen fields of the central Namib. *Vegetatio* **98:** 113–128.

Scholz, H. (1972) The soils of the central Namib Desert with special consideration of the soils in the vicinity of Gobabeb. *Madoqua* **2:** 33–51.

Seely, M. K. (1978) The Namib Dune Desert: an unusual ecosystem. *Journal of Arid Environments* **1:** 117–128.

Seely, M. K. (1984) The Namib's place among deserts of the world. *South African Journal of Science* **80:** 155–158.

Seely, M. K. & Hamilton, W. J. (1978) Durability of vehicle tracks on three Namib Desert substrates. *South African Journal of Wildlife Research* **8:** 107–111.

Sérusiaux, E. & Wessels, D. (1984) *Santessonia* (*Lecanorales*, *Buelliaceae*) in the Namib Desert (South West Africa). *Mycotaxon* 19: 479–502.

Simmons, R. E., Griffin, M., Griffin, R. E., Marais, E. & Kolberg, H. (1998) Endemism in Namibia: patterns, processes and predictions. *Biodiversity and Conservation* **7:** 513–530.

Southgate, R. I., Masters, P., & Seely, M. K. (1996) Precipitation and biomass changes in the Namib Desert dune ecosystem. *Journal of Arid Environments* **33:** 267–280.

St. Clair, L. L., Johansen, J. R. & Rushforth, S. R. (1993) Lichens of soil crust communities in the Intermountain Areas of the western United States. *Great Basin Naturalist* **53:** 5–12.

ter Braak, C. F. J. (1988) CANOCO—an extension of DECORANA to analyze species-environment relationships. *Vegetatio* **75:** 159–160.

Tuba, Z., Csintalan, Z., Szente, K., Nagy, Z. & Grace, J. (1998) Carbon gains by desiccation-tolerant plants at elevated CO_2. *Functional Ecology* **12:** 39–44.

van Zinderen Bakker, E. M. (1975) The origin and palaeoenvironment of the Namib Desert biome. *Journal of Biogeography* **2:** 65–73.

Walter, H. (1986) The Namib Desert. In *Ecosystems of the World—Hot Deserts and Arid Shrublands, 12B* (M. Evenari, I. Noy-Meir & D. W. Goodall, eds): 245–282. New York: Elsevier Science Publishing Company.

Werger, M. J. A. & Sprangers, J. T. C. (1982) Comparisons of floristic and structural classifications of vegetation. *Vegetatio* **50:** 174–183.

Wessels, D. C. J. & van Vuuren, D. R. J. (1986) Remote sensing—its possible use in mapping the distribution of major lichen communities in the Namib Desert, South West Africa. *Madoqua* **14:** 369–374.

Wessels, D. C. J., Wessels, L. A. & Holzapfel, W. H. (1979) Preliminary report on lichen-feeding Coleoptera occurring on *Teloschistes capensis* in the Namib Desert, South West Africa. *Bryologist* **82:** 270–273.

Will-Wolf, S., Scheidegger, C. & McCune, B. (2002) Methods for monitoring biodiversity and ecosystem function. In *Monitoring With Lichens—Monitoring Lichens*. (L. Nimis, C. Scheidegger & P. A. Wolseley, eds): 147–162. Netherlands: Kluwer Academic Publishers.

Wirth, V. & Vězda, A. (1975) Drei neue Flechtenarten aus Sudwestafrika. *Stuttgarter Beitrage zur Naturkunde Series A (Biologie)* **284:** 1–4.

Accepted for publication 20 *September* 2004