



**Flora of the Pro-Namib Desert Swakop River  
catchment, Namibia: community classification and  
implications for desert vegetation sampling**

Guy Cowlshaw\* & Jonathan G. Davies†

\*Department of Anthropology, University College London, Gower Street,  
London WC1E 6BT, U.K.

†Natural History Museum, Cromwell Road, London SW7 5BD, U.K.

(Received 20 October 1995, accepted 13 May 1996)

Plant assemblages were studied in the Pro-Namib Desert Swakop River catchment in Namibia (southern Africa) in order to describe the communities present. Two surveys were conducted: a stratified survey of desert and dry riverbed vegetation and a grid-based survey of desert vegetation alone. In the first survey, 'very high' growth forms (plants > 150 cm height) were recorded using eight 50 × 50 m quadrats in each of four habitats. In the second survey, all plants except grasses were split into high (plants > 50 cm) and low (plants ≤ 50 cm) growth forms and each recorded using 25 quadrats on five 2.4 km transects (one per 600 m of transect) placed in parallel, 2 km apart (with minimum quadrat size determined by the nested quadrats method). Data from both surveys were analysed using standard classification (TWINSPAN) and ordination (DECORANA) techniques. These analyses were conducted for species and quadrats, both (1) with and without outliers (both cases), and (2) with and without downweighting of rare species (species only). However, the ecological interpretation of the results remained consistent throughout. Results from the stratified survey revealed distinct plant communities; (1) riparian woodland characterized by *Prosopis glandulosa* and *Salvadora persica*, and (2) desert scrub characterized by *Acacia reficiens*, *Commiphora glaucescens* and *C. virgata*. Sub-communities in desert scrub were also recognized; these were plain and hill assemblages, distinguished by the presence or absence of *Phaeoptilum spinosum*, respectively. These communities match geomorphological features of the desert landscape and may reflect differences in the availability of moisture. However, these communities were largely undetectable in the analyses of the grid-based survey dataset, which suggests that the scale of that survey was inadequate for the purpose of classification, despite the attainment of plateaus on the species-area curves for quadrats. These results therefore draw attention to the problems of rarity and scale in the study of desert plant communities.

©1997 Academic Press Limited

**Keywords:** Namib Desert; plant community; classification; ordination

### Introduction

In habitats where only a relatively small number of species exist, it would seem, intuitively, that community classification and an understanding of the ecological processes involved would be easier to achieve than in areas of high diversity and complexity. However, plant communities in arid environments are often more difficult to define or classify than those in more species-rich habitats (e.g. Dasti & Agnew, 1994). This is particularly true for ephemeral species, whose presence is highly dependent on the irregular and unpredictable nature of physical conditions in potentially 'nonequilibrium' arid land ecosystems (see Wiens, 1984; DeAngelis & Waterhouse, 1987). Walter (1986) has consequently argued that the classification of desert ecosystems may be more effectively achieved through geomorphological features rather than through vegetation. However, perennial desert species are longer-lived and appear to exist in relatively stable communities (e.g. Vasek, 1980; Goldberg & Turner, 1986), thus providing the foundation for a classification of the vegetation communities themselves. Nevertheless, the water requirements of these species and their ability to compete for soil moisture (e.g. Fowler, 1986; Yeasler & Esler, 1990) may yet lead to a correlation between particular species and geomorphological features of different water-retaining characteristics.

The purpose of this study is to explore plant assemblage definition in an area of the Pro-Namib Desert Swakop River catchment in Namibia. Its main aim is to describe the plant communities which are present, and thereby provide an initial basis for the future study of the ecological processes in this area. In addition, the opportunity to consider the connection between species and geomorphological features will be briefly explored. Finally, this analysis provides a salutary reminder of the problems of rarity and scale in the analysis of desert plant communities.

The Namib Desert is a narrow strip of land between 80–150 km wide which stretches for almost 2000 km along the south-west coast of Africa. It is bordered to the north by the San Nicolai River (Angola) and to the south by the Olifants River (South Africa) (Walter, 1986). Its plant life constitutes an important component of the Karoo-Namib flora, which is unusually diverse and distinctive with several endemic species (e.g. Archibold, 1995). In addition, the Namib Desert may be one of the oldest deserts in the world (Ward *et al.*, 1983). Consequently, its plant life may have had longer to evolve under arid conditions and to specialize into various microhabitat niches than those species found in deserts elsewhere (Günster, 1994). This in turn means that of all desert plant communities around the world, it is those in the Namib which might be most likely to give rise to easily definable and distinct sub-communities. This makes the Namib flora a particularly appropriate focus for the current study.

Previous classification of Namibian flora have been attempted, although primarily at the macroecological level. Giess (1971) provided the first classification and vegetation map of Namibia, which is still widely used today (e.g. van der Merwe, 1983; Müller, 1984; Moyo *et al.*, 1993). According to this classification, the present study is conducted in the semi-desert and savanna transition (escarpment zone) region of the Namib Desert, which also incorporates areas of riverine woodland. More recently, Jürgens (1991) has revised existing broader classifications of the larger Karoo-Namib region, which places the current study area in the Namaland subdomain of the Nama Karoo phytogeographical unit. At a more detailed level, Walter (1986) identifies nine different biotopes within the Namib Desert. These are classed in Outer and Inner Namib groups and are based primarily on geomorphological features. The present study appears to span three of these biotopes; the oases of the large 'alien' riviere, the monadnocks (i.e. inselbergs, or koppies) and riviere of the inner Namib, and finally the pre-Namib. The pre-Namib closely matches the savanna transition zone identified above; both of these regions are treated under the heading of the Pro-Namib for the purposes of this analysis. The current study follows Sullivan (1993) in attempting to

d  
q  
a  
l  
  
T  
re  
ar  
ep  
to  
pr  
gr  
Ar  
va  
rai  
be  
Di  
to  
rea

Figur  
throu  
Wind

develop a classification of different plant communities in the Pro-Namib desert using quantitative numerical techniques. The approach adopted is that of complementary analysis, using both classification and ordination procedures (see Kent & Ballard, 1988).

## Methods

### Study site

The study was conducted at Tsaobis Leopard Park, a wildlife reserve in the Karibib region of Namibia, Southern Africa (Fig. 1). The reserve is dominated by mountains and ravines fringed by steep foothills and rolling plains, bordered to the north by the ephemeral Swakop River. The reserve encompasses a total area of 45,000 ha and a topographical range of 683–1445 m altitude. Geologically, the area is composed primarily of metamorphosed Nosib and Damara sediments, intruded by post-Damara granites and pegmatite bodies (Bothe, 1980). The climate is arid and unpredictable. Annual rainfall since 1900 in this region has a mean of 202 mm and a coefficient of variation of 52% (data from Karibib, 40 km north of Tsaobis; Fig. 2). Mean annual rainfall at Tsaobis itself is lower still (85 mm:  $N = 5$  years) and typically occurs only between January and April (Fig. 3; note that only an annual total is available for 1989). During the study year (1991), rainfall was low at 56 mm and the Swakop River failed to flow here. Ground fog and dew are also rare, while coastal fogs do not appear to reach this far inland (see Walter, 1986). Monthly variation in shade temperature is

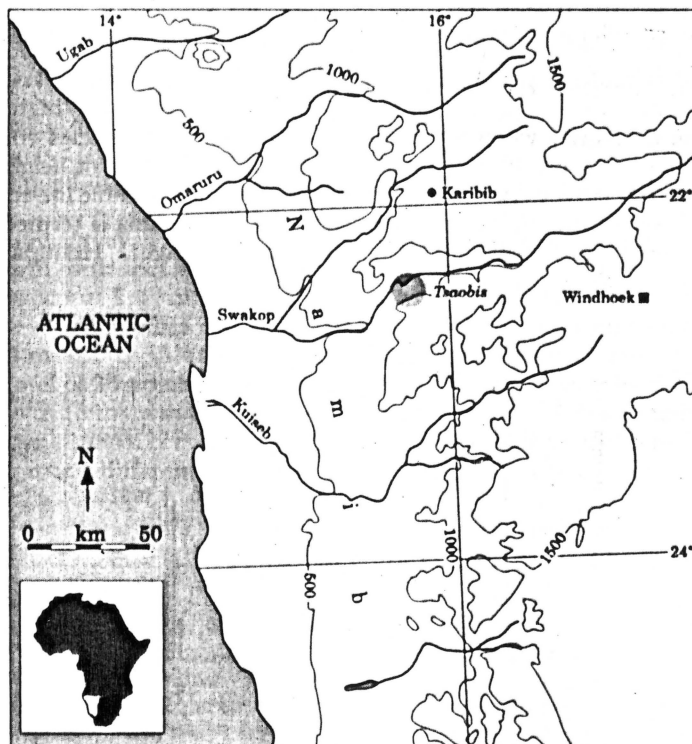


Figure 1. Map of the central Namib Desert illustrating the main ephemeral rivers which run through this region and the location of the study site. The town of Karibib and the capital Windhoek are also shown.

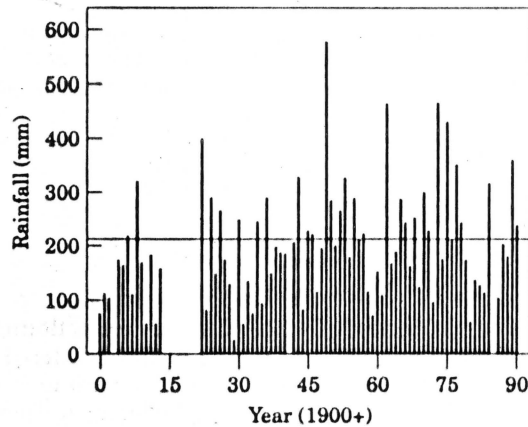


Figure 2. Annual rainfall at Karibib between 1900-1991. The horizontal line shows the mean value.

plotted in Fig. 4 (Karibib means, calculated from 1967-1983). Temperatures at Tsaobis were somewhat warmer and have not been known to drop below  $0^{\circ}\text{C}$  ( $N = 5$  years).

#### Survey procedures

Many different life-forms were recognized in our sample, including woody perennial, ephemeral and succulent species. For the purposes of community classification, we split the plants into two basic growth forms: 'low' ( $< 50$  cm) and 'high' ( $\geq 50$  cm). Although these categories were not exclusive, since the same species could occur in both groups depending on the size range of individuals, the use of height provides a simple and objective survey criterion which encompasses all possible life-forms. A third category, a sub-set of the high forms, was also recognized; this is termed 'very high' and includes only those specimens  $> 150$  cm in height. Hemiparasites (e.g.

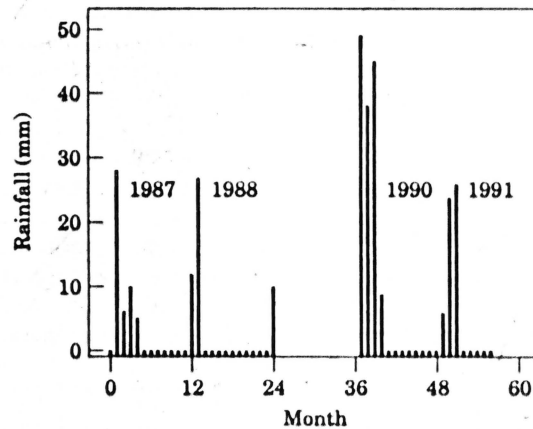


Figure 3. Monthly rainfall at Tsaobis between 1987-1991. Monthly data are not available for 1989. Month 1 is January. (Note that annual rainfall is calculated from July to June in the text).

Figur  
most

Tapi  
was  
initia  
role o

Tw  
samp  
the st  
Bed o  
logica  
m x  
of ver  
theref  
(Octo

In t  
and lo  
site, fi  
of 2 k  
range  
interv  
and lo  
Golds  
were r

Swak  
Swak  
Nami  
Nami

N=8

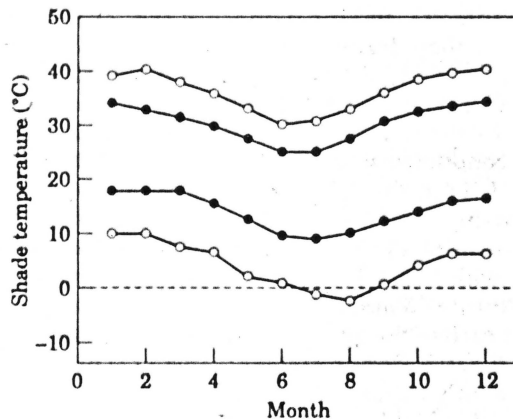


Figure 4. Shade temperature variation (Karibib). Minima and maxima mean average (●) and most extreme value (○) are shown. Data from 1969–1983. Month 1 is January.

*Tapinanthus oleifolius* (Wendl.) Danser) were listed in the category in which their host was recorded. However, grasses were excluded from the survey, since this study initially began as an adjunct to research in baboon evolutionary ecology wherein the role of grasses is minimal at this site.

Two surveys were conducted, using (1) stratified sampling and (2) grid-based sampling methods. In the first survey, four distinctive habitat types were identified in the study area; these were the Hills and Plains of the Namib and the Woodland and Bed of the Swakop River. Their identification was made on the basis of geomorphological and plant physiognomic features (Table 1). In each of these habitats, eight 50 m × 50 m quadrats were randomly placed (a total of 32 quadrats) and all specimens of very high growth form species were recorded. A total area of 2 ha of each habitat was therefore sampled. This survey was conducted towards the end of the austral winter (October).

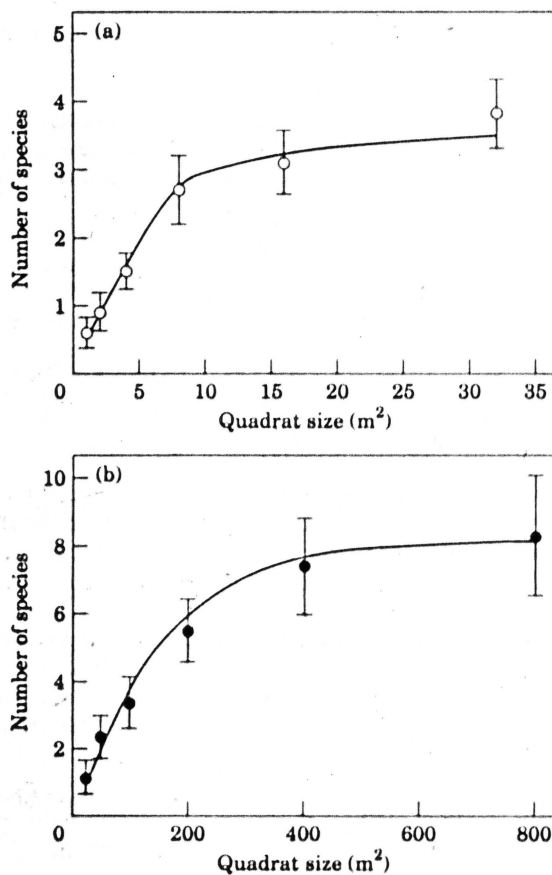
In the second survey, a sampling grid was developed to record the abundance of high and low growth form species in the Namib Hills and Plains habitats. Across the study site, five transects of 2.4 km were marked out in parallel, each separated by a distance of 2 km. The grid therefore encompassed an area of about 19 km<sup>2</sup> and an altitudinal range of 750 m–950 m. Along each transect, sampling points were located at 600-m intervals (a total of 25 points). The minimum quadrat size necessary for sampling high and low growth forms was determined using the nested quadrats method (following Goldsmith *et al.*, 1986). Hence, for each vegetation category, six different quadrat sizes were nested at ten different sampling points (randomly chosen across the grid, but

Table 1. Physiognomic features of the four habitat types

Habitat	Predominant vegetation	Predominant substrate	Ground slope
Swakop Bed	None	Loose sand	0° –
Swakop Woodland	Riparian woodland	Loose sand	0° (0°–10°)
Namib Plains	Desert scrub	Sand/gravel/rock	0° (0°–30°)
Namib Hills	Desert scrub	Sand/gravel/rock	45° (30°–70°)

N=8 for ground slope measure; median (and range in parenthesis).

occurring on all five transects), and the number of species in each quadrat recorded. Species-area curves were then drawn and the quadrat size determined from the area beyond which the number of additional species was minimal (Fig. 5). Quadrat size for low growth forms was therefore 2 m × 4 m, resulting in a total survey area of 200 m<sup>2</sup>; quadrat size for high growth forms was 20 m × 20 m, generating a total survey area of 1 ha. This survey was conducted at the height of the wet season (April) to ensure that ephemerals were recorded together with the perennial species in the sample (although since the rains poor few ephemerals were recorded; see below). The presence, identity and height of all specimens of all species was recorded, through the use of keys in the field and consultation with Herta Kolberg and Coleen Mannheimer of the National Botanical Research Institute, Windhoek. Following the survey, it was also possible to retrospectively allocate each of the grid quadrats to either Plains or Hills habitats using the criteria adopted in the stratified survey (see Table 1). This revealed that eight of the Namib grid survey quadrats fell in Plains habitats and 15 fell in Hills areas (the two remaining were intermediate and so discounted from either category).



**Figure 5.** Species-area curves for determining minimum quadrat size for the grid survey of (a) low and (b) high growth forms. Mean species richness values are plotted with standard error bars and the curves are drawn by eye. The quadrat sizes selected for sampling were 8 m<sup>2</sup> and 400 m<sup>2</sup> for low and high growth forms, respectively.

### Data analysis

Identification of plant communities was carried out using Two-Way Indicator Species Analysis (TWINSPAN: Hill, 1979a; Gauch & Whittaker, 1981). This is a divisive polythetic method of plant community classification which hierarchically divides a set of either species or quadrats into a series of several related sub-groups (the method is fully explained in Kent & Coker, 1992). In the present analyses, the density (rather than presence-absence) of species was used as the basis of the classification, and the stopping criterion for division was set at a minimum requirement of five items per group with no more than five divisions on any one branch. Four TWINSPAN analyses are discussed here. These are the classifications of the very high growth form species in the stratified survey, and the low, high and the subset of very high growth form species in the grid survey. The analyses of quadrats are also discussed, but emphasis is given to the species classification because only limited environmental data were collected to compare with the quadrat patterns. In all TWINSPAN analyses divisions with eigenvalues below 0.15 are discarded (together with all other subsequent divisions). In order to aid the interpretation of the TWINSPAN results, and in particular to ensure that this method had not produced an arbitrary classification (imposing discrete groups on a continuous distribution), the data were also analysed using the ordination technique of Detrended Correspondance Analysis (DECORANA: Hill, 1979b; Hill & Gauch, 1980). This method is also fully explained in Kent & Coker (1992).

### Results

Plant species abundances and their TWINSPAN associations at Tsaobis are given in Tables 2 and 3 for the stratified and grid-based surveys, respectively. The dendrograms of these analyses, indicating the relationships between the different classified groups, are shown in Fig. 6. In two cases (the low and very high growth form species of the grid survey), the datasets were skewed by the presence of outlying quadrats; these were quadrats which were entirely empty except for the presence of a species which was otherwise unrecorded in that survey. In the low growth forms, there were two outlying quadrats, possessing a *Protasparagus* sp. and a seedling *Combretum apiculatum* Sond.; in the very high growth forms, it was a single quadrat with several specimens of *Acacia senegal* Willd var *Rostrata*. The analyses presented here are those in which these outliers were removed from the dataset; however, the same analyses were also run with these quadrats and results of a similar nature were obtained, although the TWINSPAN groups were less well defined. The TWINSPAN analyses were also run twice, where (1) equal weighting was given to all species (the standard run; outliers removed as described) and (2) rare species were downweighted (in which case the outliers were included). The results of both runs are described below.

#### *Stratified survey of very high growth form species*

The first division in this TWINSPAN analysis is extremely well-supported with an eigenvalue of 0.99 (Fig. 6(a)). Two further divisions produce a total of four different groups in the stratified survey of very high growth form species. The ordination of this dataset (Fig. 7) broadly corroborates the classification. Group D (which might be denoted as common Swakop habitats species) is clearly discrete from the Group A-C cluster (common Namib habitats species). TWINSPAN and DECORANA analysis of the quadrats (which produces an identical pattern) reveals that the second division (along Axis 2) reflects a distinction between the Namib Hills and Namib Plains habitat types: five of the six quadrats in the group which is analogous to the A + B cluster are sited in the Plains and seven of the eight quadrats in the analogous group C cluster are

t recorded.  
m the area  
rat size for  
of 200 m<sup>2</sup>;  
vey area of  
ensure that  
(although  
e, identity  
keys in the  
National  
ossible to  
itats using  
ight of the  
s (the two

vey of (a)  
error bars  
d 400 m<sup>2</sup>

Table 2. Plant species of the stratified very high growth forms survey. \* Taxa are listed in alphabetical order of family and then species

No.	TWINSPAN Group (a)	Family	Species	Swakop		Namib	
				Bed 2 ha <sup>-1</sup>	Woodland 2 ha <sup>-1</sup>	Plains 2 ha <sup>-1</sup>	Hills 2 ha <sup>-1</sup>
1	B	Bignoniaceae	<i>Catophractes alexandri</i>	—	—	6	1
2	C	Burseraceae	<i>Commiphora glaucescens</i>	—	—	3	23
3	C	Burseraceae	<i>Commiphora saxicola</i>	—	—	3	10
4	B	Burseraceae	<i>Commiphora virgata</i>	—	—	5	3
5	B	Capparaceae	<i>Boscia albitrunca</i>	—	—	1	—
6	A	Capparaceae	<i>Boscia foetida</i>	1	—	3	3
7	C	Combretaceae	<i>Combretum apiculatum</i>	—	—	1	1
8	D	Ebenaceae	<i>Euclea pseudebenus</i>	—	7	—	—
9	C	Euphorbiaceae	<i>Euphorbia virosa</i>	—	—	1	1
10	D	Fabaceae	<i>Faidherbia albida</i>	1	8	—	—
11	D	Fabaceae	<i>Acacia erioloba</i>	—	2	1	—
12	B	Fabaceae	<i>Acacia erubescens</i>	—	—	12	6
13	C	Fabaceae	<i>Acacia mellifera</i>	—	—	2	—
14	C	Fabaceae	<i>Acacia reficiens</i>	1	—	4	9
15	C	Fabaceae	<i>Acacia senegal</i>	—	—	—	1
16	D	Fabaceae	<i>Acacia tortilis</i>	1	1	—	—
17	D	Fabaceae	<i>Prosopis glandulosa</i>	6	49	1	—
18	†	Loranthaceae	<i>Tapinanthus oleifolius</i>	1	15	—	—
19	B	Nyctaginaceae	<i>Phaeoptilum spinosum</i>	—	—	12	1
20	D	Salvadoraceae	<i>Salvadora persica</i>	2	22%	2	—
21	C	Sterculiaceae	<i>Sterculia africana</i>	—	—	—	2
22	D	Tamaricaceae	<i>Tamarix usneoides</i>	—	9%	—	—
23	B	Unknown	Unidentified 1	3	0	0	0
24	D	Unknown	Unidentified 2	6	7	0	0

\*Where individual plants are not discernible, % ground cover is listed.

†Hemiparasite on *P. glandulosa* and infrequently *S. persica*.

Table 3. Plant species of the grid-based Namib survey (low and high growth forms, gD). Taxa are listed in alphabetical order of family (except Fabaceae and Asparagaceae) and then species. Columns show (1) individual code, (2) TWINSPAN group identity, (3) family and species name and (4) the frequency (number of low-high growth form quadrats in which it occurs) and density (number of specimens over the area of



\*Where individual plants are not discernible, % ground cover is listed.  
 †Hemiparasite on *P. glandulosa* and infrequently *S. persica*.

**Table 3.** Plant species of the grid-based Namib survey (low and high growth forms, gf). Taxa are listed in alphabetical order of family (except Fabaceae and Asparagaceae) and then species. Columns show (1) individual code, (2) TWINSPAN group identity, (3) family and species name and (4) the frequency (number of low-high growth form quadrats in which it occurs) and density (number of specimens over the area of the low and high growth form survey). Asterisks show outliers removed from the analyses (see Results)

No.	TWINSPAN Group (Fig. 6)			Family	Species	Freq. High gf -Low gf (N)	Density	
	(b)	(c)	(d)				High gf survey (ha <sup>-1</sup> )	Low gf survey (200 m <sup>-2</sup> )
1	-	L	-	Acanthaceae	<i>Barleria damarensis</i>	02-00	2	0
2	K	M	-	Acanthaceae	<i>Barleria prionitoides</i>	02-01	4	1
3	K	L	-	Acanthaceae	<i>Blepharis obmitrata</i>	01-01	1	5
4	E	N	-	Acanthaceae	<i>Monechma cleomoides</i>	02-02	2	3
5	G	N	-	Acanthaceae	<i>Petalidium variable</i>	08-02	19	2
6	-	L	-	Acanthaceae	<i>Ruellia diversifolia</i>	02-00	2	0
7	H	-	-	Aizoaceae	<i>Corbichonia decumbens</i>	00-02	0	2
8	I	-	-	Aizoaceae	<i>Gisekia africana</i>	00-07	0	18
9	K	-	-	Aizoaceae	<i>Mollugo cerviana</i>	00-01	0	2
10	-	N	-	Amaranthaceae	<i>Leucosphaera bainesii</i>	05-00	7	0
11	F	P	-	Amaranthaceae	<i>Calicorema capitata</i>	11-01	32	1
12	-	L	-	Amaranthaceae	<i>Marcellioopsis denudata</i>	01-00	1	0
13	-	L	-	Anacardiaceae	<i>Rhus marlothii</i>	01-00	1	0
14	-	L	-	Asclepiadaceae	<i>Orthanthera albida</i>	02-00	2	0
15	K	-	-	Asteraceae	<i>Dicoma cf. schinzii</i>	00-02	0	3
16	K	-	-	Asteraceae	<i>Geigeria cf. acaulis</i>	00-01	0	7
17	-	N	Q	Fabaceae	<i>Acacia erubescens</i>	04-00	8	0
18	G	L	Q	Fabaceae	<i>Acacia mellifera</i>	02-01	3	1
19	-	P	T	Fabaceae	<i>Acacia reficiens</i>	02-00	6	0
20	-	N	*	Fabaceae	<i>Acacia senegal</i>	01-00	12	0
21	-	N	-	Fabaceae	<i>Adenolobus garipensis</i>	01-00	2	0
22	F	-	-	Fabaceae	<i>Crotalaria argyrea</i>	00-03	0	11
23	J	L	-	Fabaceae	<i>Indigofera adenocarpa</i>	05-07	35	18

Table 3. (continued)

No.	TWINSPAN Group (Fig. 6)			Family	Species	Freq. High gf -Low gf (N)	Density	
	(b)	(c)	(d)				High gf survey (ha <sup>-1</sup> )	Low gf survey (200 m <sup>-2</sup> )
24	I	-	-	Fabaceae	<i>Indigofera cf. teixeirae</i>	00-06	0	7
25	I	L	-	Fabaceae	<i>Psycholobium biflorum</i>	01-03	1	10
26	-	N	-	Fabaceae	<i>Rhynchosia candida</i>	01-00	1	0
27	F	-	-	Fabaceae	<i>Tephrosia dregeana</i>	00-03	0	39
28	G	N	-	Bignoniaceae	<i>Catophractes alexandri</i>	01-01	29	2
29	-	N	T	Burseraceae	<i>Commiphora glaucescens</i>	10-00	18	0
30	-	N	S	Burseraceae	<i>Commiphora saxicola</i>	07-00	7	0
31	K	M	S	Burseraceae	<i>Commiphora virgata</i>	21-02	95	3
32	-	M	R	Capparaceae	<i>Boscia foetida</i>	12-00	18	0
33	-	N	-	Capparaceae	<i>Boscia sp.</i>	01-00	1	0
34	G	P	-	Capparaceae	<i>Cleome suffruticosa</i>	03-05	8	11
35	*	-	-	Combretaceae	<i>Combretum apiculatum</i>	00-01	0	2
36	F	L	-	Euphorbiaceae	<i>Chamaesyce glanduligera</i>	01-11	1	27
37	-	L	Q	Euphorbiaceae	<i>Euphorbia virosa</i>	02-00	2	0
38	*	L	-	Asparagaceae	<i>Protasparagus sp.</i>	02-01	3	1
39	K	L	-	Malvaceae	<i>Gossypium anomalum</i>	03-01	5	1
40	K	L	-	Malvaceae	<i>Hibiscus elliotiae</i>	05-01	11	1
41	-	N	Q	Nyctaginaceae	<i>Phaeoptilum spinosum</i>	02-00	4	0
42	-	O	T	Periplocaceae	<i>Curroria decidua</i>	12-00	23	0
43	-	N	-	Polygalaceae	<i>Polygala guerichiana</i>	01-00	1	0
44	E	-	-	Portulacaceae	<i>Portulaca kermesina</i>	00-03	0	5
45	K	-	-	Portulacaceae	<i>Talinum cf. arnotii</i>	00-01	0	2
46	K	L	-	Rubiaceae	<i>Amphiasma divaricanum</i>	02-01	4	7
47	-	L	-	Rutaceae	<i>Thamnosma africana</i>	01-00	1	0
48	K	-	-	Sterculiaceae	<i>Hermannia modesta</i>	00-04	0	19

Table 3. (continued)

No.	TWINSPAN Group (Fig. 6)			Family	Species	Freq. High gf -Low gf (N)	Density	
	(b)	(c)	(d)				High gf survey (ha <sup>-1</sup> )	Low gf survey (200 m <sup>-2</sup> )
49	-	L	-	Verbenaceae	<i>Chascanum garipense</i>	01-00	2	0
50	E	-	-	Zygophyllaceae	<i>Tribulus zeyheri</i>	00-04	0	15
51	K	-	-	Unknown	unidentified 3	01-05	3	16
52	K	-	-	Amaranthaceae	<i>Nelsia quadrangula</i>	00-01	0	1

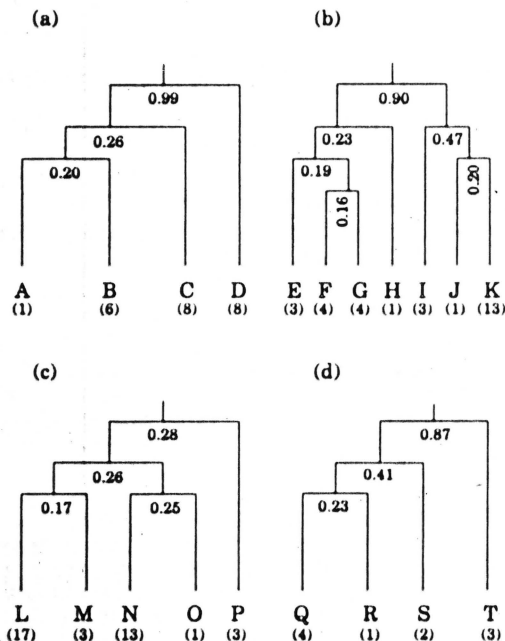
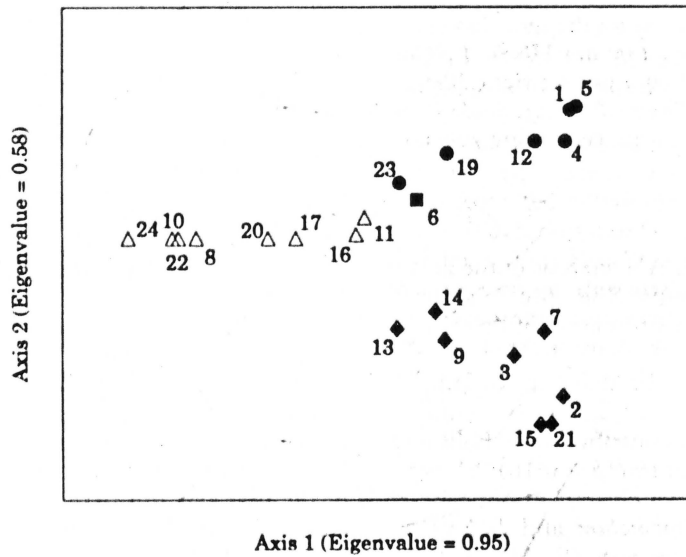


Figure 6. TWINSpan dendrograms of the hierarchical division of (a) the stratified survey of very high growth forms; and the grid-based surveys of (b) low growth forms, (c) high growth forms and (d) very high growth forms. Eigenvalues are shown at each division, and the letters A-T are used to denote the identity of the different groups obtained (see Tables 2 and 3). Numbers in brackets show the number of species in each group.

sited in the Hills (Fisher's exact test:  $p < 0.05$  two-tailed). The indicator species identified in this TWINSpan analysis are (1) *Prosopis glandulosa* Torr. (an alien invasive species in Namibia) and *Salvadora persica* L. for the Swakop habitats and *Acacia reficiens* Wawra & Peyr., *Commiphora glaucescens* Engl. and *C. virgata* Engl. for the Namib habitats (at the first division); and (2) *Phaeoptilum spinosum* Radlk. for the Namib Plains habitat (at the second division). Note that in this case the final TWINSpan division (between groups A and B) is not verified in the ordination. Finally, a second ordination of this sample but with downweighting applied to rare species produced a similar pattern, but in this case the Swakop and Namib groups were distantly separated and the division within the Namib group was lost. The implications of this result for the community classification are considered in the Discussion.

#### Grid survey of low growth form species

The TWINSpan analysis of the grid survey of low growth form species also exhibited a strong first division and produced seven well-defined groups (Fig. 6(b)). The DECORANA ordination (Fig. 8) supported this classification, but only to a limited degree. The first division of the species groups (E-H vs. I-K) produced discrete clusters, but their spatial separation was minimal (less than that seen within groups). Ordination of the quadrats produced a similar pattern. Investigation of whether this first division reflected a discrimination between habitat types as seen above (through the *post hoc* designation of these quadrats into Hills and Plains categories) revealed that there was a pattern of weak statistical significance (Fisher's exact test:  $p = 0.07$  two-tailed) with Hills quadrats predominating in groups analogous to the species groups I-K. Downweighting of rare species had little effect on this ordination; the division was

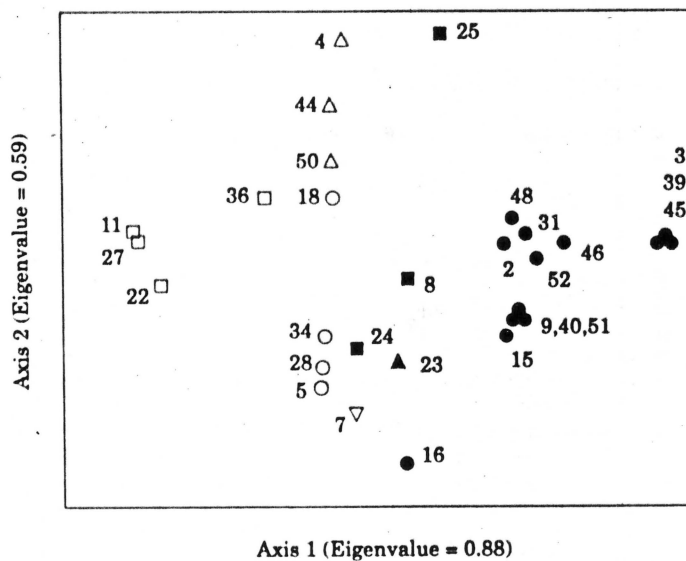


**Figure 7.** DECORANA ordination of the very high growth form species of the stratified survey. Each species is numbered (Table 2) and the symbols represent the different TWINSPAN groups (Fig. 6(a)): group A (■), group B (●), group C (◆) and Group D (△). Note that the distinction between solid and open symbols reflects those species separated at the first division.

survey of  
gh growth  
the letters  
2 and 3).

r species  
(an alien  
itats and  
Engl. for  
c. for the  
the final  
ordination.  
d to rare  
up were  
lications  
on.

hibited  
)). The  
limited  
discrete  
groups).  
ther this  
through  
led that  
07 two-  
groups  
sion was



**Figure 8.** DECORANA ordination of the low growth forms of the grid-based survey. Each species is numbered (Table 3) and the symbols represent the different TWINSPAN groups (Fig. 6(b)): group E (△), group F (□), group G (○), group H (▽), group I (■), group J (▲) and group K (●). Note that the distinction between solid and open symbols reflects those species separated at the first division.

unchanged although the two clusters of species at opposite ends of the first axis (on the left *Calicorema capitata* Hook. f., *Crotalaria argyrea* Welw. ex Baker and *Tephrosia dregeana* E. Mey.; on the right *Blepharis obmitrata* C.B. Clarke, *Gossypium anomalum* Wawra ex Wawra & Peyr, and *Talinum* cf. *arnotii* Hook. f.) became more clearly separated from the remaining species.

#### Grid survey of high growth form species

The TWINSPAN analysis of the grid survey of high growth form species produced five different groups (Fig. 6(c)), although the eigenvalues for all divisions were low ( $< 0.30$ ). The ordination of these data did not confirm the discrete existence of any of these groups (Fig. 9). Indeed, there was considerable overlap of the TWINSPAN groups across the diagram, despite eigenvalues of reasonable value along each axis. Ordination of the quadrats was equally ambiguous; once again, there was no difference in the relative contribution of Hills and Plains samples to the two main quadrat groups (Fisher's exact test:  $p > 0.10$ ). The only notable feature of the species ordination is the presence of two clusters at opposite ends of the first axis (on the left *Acacia mellifera* Benth., *G. anomalum* and *Indigofera adenocarpa* E. Mey.; on the right *A. senegal*, *Adenolobus garipensis* (E. Mey.) Torre & Hillc. and *Rhynchosia candida* (Welw. ex Hiern) Torre). Downweighting of rare species only served to emphasize these clusters.

#### Grid survey of very high growth form species

Given the distinct division within the stratified sample of very high growth form species between Namib Hills and Namib Plains areas, it is perhaps surprising that the grid survey, of high growth form species did not produce clearer results. In order to

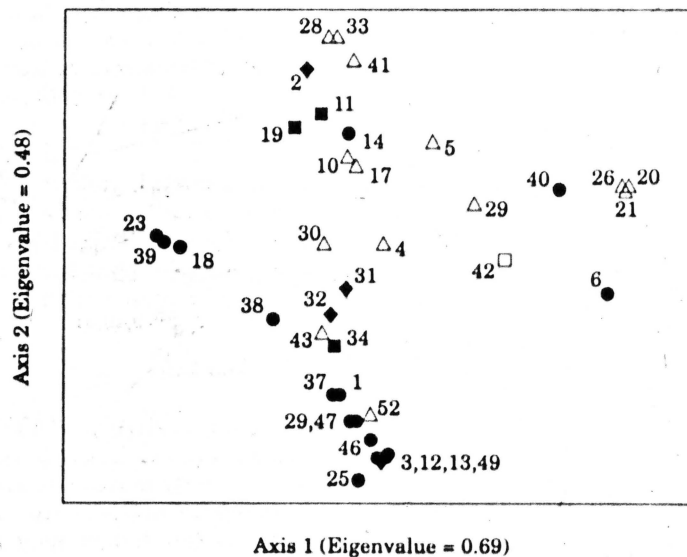


Figure 9. DECORANA ordination of the high growth forms of the grid-based survey. Each species is numbered (Table 3) and the symbols represent the different TWINSPAN groups (Fig. 6(c)): group L (●), group M (◆), group N (△), group O (□) and group P (■). Note that the distinction between solid and open symbols reflects those species separated at the first division.

investigate this further, the high growth forms grid survey data were re-analysed following the removal of all plant specimens  $\leq 1.5$  m in height. This procedure rendered the Namib grid survey now directly comparable to the stratified all-habitats survey, i.e. only very high growth form species were under consideration. The TWINSpan analysis of the edited dataset produced four groups as opposed to five, with one strong division which separated the first group (comprising *A. reficiens*, *C. glaucescens* and *Curroria decidua* Planch. ex Benth.) from the remaining groups (Fig. 6(d)). While DECORANA ordination confirmed this separation it did not support any of the subsequent TWINSpan divisions of this dataset (Fig. 10). Downweighting of rare species did not alter these findings. A comparison of this analysis with the stratified survey reveals the following. First, that there are consistent associations across the two analyses between (1) *C. glaucescens* and *A. reficiens*; (2) *Acacia erubescens* Welw. ex Oliver and *P. spinosum*; and (3) *Euphorbia virosa* Willd. and *A. mellifera* (see Tables 2 and 3). Second, despite these associations, there is no general resemblance between the TWINSpan groups of the two analyses, with the exception that *Boscia foetida* Schinz consistently appears in its own group (Groups A and R in the stratified and current analyses, respectively).

Discussion

The preceding results indicate a relatively homogeneous habitat with few distinct associations. Before discussing the patterns of species assemblages which emerged from this analysis, it is first necessary to consider briefly the effects of species rarity and patchiness in these classifications.

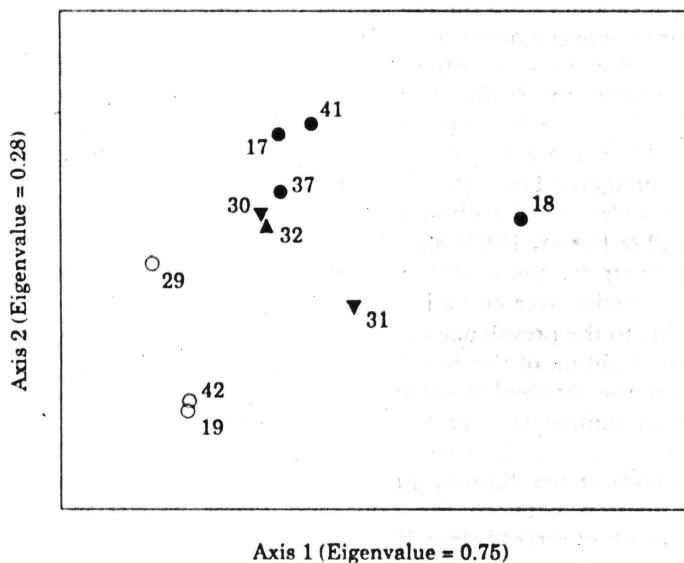


Figure 10. DECORANA ordination of the very high growth form species of the grid-based survey. Each species is numbered (Table 3) and the symbols represent the different TWINSpan group (Fig. 6(d)): group Q (●), group R (▲), group S (▼) and group T (○). Note that the distinction between solid and open symbols reflects those species separated at the first division.

*The role of rarity and patchiness*

The rarity of species within the grid survey of the Namib habitats was marked (see Table 3). A total of 31 low growth form species and 39 high growth form species were identified (including 17 species which appeared in both of these classes), but of these approximately 25% were recorded on the basis of one specimen only in their respective surveys (seven and nine species, respectively). It is only a similar fraction which occurs in more than five quadrats (i.e. 20% of the survey area) (six and ten species, respectively).

Several species were also extremely patchy in their distribution. In the low growth form grid survey, *T. dregeana* occurred in only three quadrats but in one of these 31 individuals were recorded (the next most locally abundant herb only achieved an abundance of 11 individuals in any one quadrat). In the high growth form survey, both *A. senegal* and *Catophractes alexandri* D. Don were recorded in only one quadrat, but at individual densities of 12 and 28, respectively. Patchiness of this kind is likely to influence the shape of the species-area curve, since it should affect the rate at which new species are detected with increasing sample area. This can be examined by comparing the species-area curves of the sample with a theoretical species-area curve based on probability theory (following Hubbell & Foster, 1983; Mutangah & Agnew, 1996). This curve is calculated on the assumption of a random dispersion of individuals for each species, using the equation:

$$s(a) = S - \sum (1-a)^{n(i)}$$

where  $s$  is the mean number of species for a fractional area of the sample  $a$ ,  $S$  is the total number of species in the sample and there are  $n(i)$  individuals of the  $i$ th species in the sample. The theoretical curves for the low and high growth form grid surveys are compared against the actual curves in Fig. 11 (where the actual curves are based on the mean value of ten different combinations of the required number of quadrats at each point, drawn at random from the full sample of 25 quadrats). In both cases, there is a marked disparity between observation and prediction, with the observed accumulation of species occurring at a substantially slower rate: the lag between the two at one-fifth of the total sample area is about five species in both low and high growth forms. Consequently, if species dispersion was even, then the number of species recorded in this area would increase by about one-third. Although the two lines inevitably converge, the predicted line typically falls outside the standard error of the observed points in both cases. Similar observations have also been made in Panamanian rain forest (Hubbell & Foster, 1983) and Kenyan dry forest (Mutangah & Agnew, 1996). This finding illustrates the potential importance of uneven dispersion of species in describing the species-area curve in different communities.

It may be due to the prevalence of both rarity and patchiness throughout the survey that the downweighting of the rarest species tended to have a minimal effect on the association patterns obtained in either the low or high growth form datasets. However, in the stratified sample of very high growth form species, the change in pattern following downweighting did suggest two facts. First, common species occurred in either the Swakop or the Namib, but rarer species were not so easily grouped; and second, the division between the Hills and Plains vegetation communities was primarily the result of rarer species. These results indicate that the rarer species of the very high growth form category may be more discriminating in their habitat requirements, revealing subtle ecological gradients within and between those already shown by the more common species. This means that rare species are providing information which may be particularly useful for the purposes of classifying these communities and perhaps also understanding the ecological processes which underlie them (see below; see also Gaston, 1994).

The c  
growth  
interp  
any co  
many  
condit  
The  
one (c  
presur  
Swako  
observ  
Mey.  
drough  
(and p  
Inter  
outlier

Figure  
based s  
species-  
error ba



Community interpretation

The clearest associations emerged from the stratified survey, among the very high growth form species in distinct habitat types. A preliminary attempt may be made at interpreting the ecological processes which underlie these patterns, although inevitably any conclusions must remain tentative given both the paucity of autecological data for many of these species and the absence of quantitative data describing environmental conditions in the survey areas.

The first division in this group, between Namib and Swakop habitats, is a reliable one (high eigenvalues in both TWINSpan and DECORANA analyses) which presumably reflects the well-established presence of ground-water stores beneath the Swakop river (e.g. Walter, 1986). Support for this inference is provided by the observation that, within the Swakop species, the drought-tolerant *Acacia erioloba* E. Mey. (species 11) spatially adjoins the Namib arid-adapted species clusters, while the drought-sensitive *Faidherbia albida* (Delile) A. Chev. (species 10) sits at the opposite (and presumably wetter) end of the Swakop cluster (see Ward & Breen, 1983). Interestingly, the strongly halophytic habit of *Tamarix* does not appear to make it an outlier in relation to the other, non-halophilous species in the Swakop. This is probably

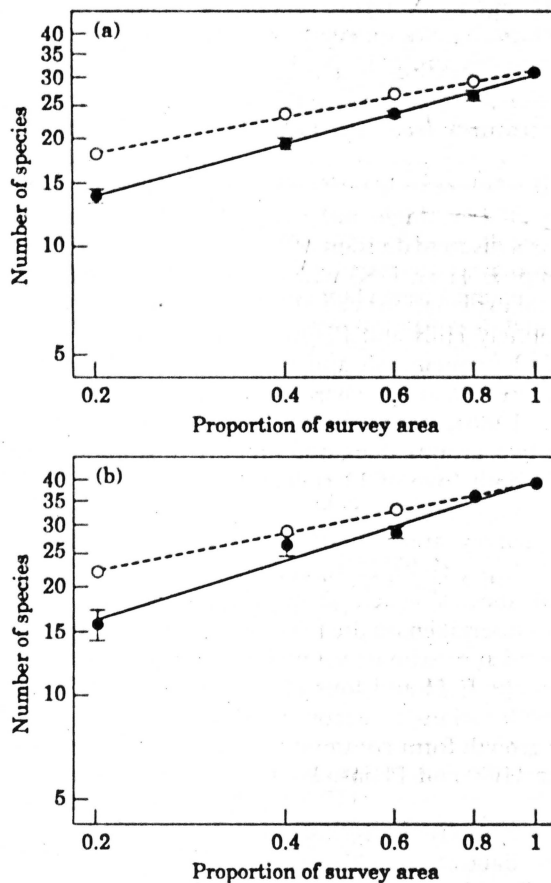


Figure 11. Species-area log-log plots for (a) the low and (b) the high growth forms of the grid-based survey. The theoretical species-area curve is shown by the dotted line (O), the observed species-area curve is shown by the solid line (●). The observed means are plotted with standard error bars.

because this species is growing on surface salt crusts and not utilizing the deeper, fresher ground-water which is exploited by other Swakop trees (see Walter, 1986).

The ecological factor/s responsible for the subsequent division between Namib Hills and Plains areas in the same sample are less easy to identify. Altitude is unlikely, given the limited topographical variation at the site. However, a fine sandy substrate, as opposed to a coarser base, might be the key factor. Indeed, four of the eight Plains quadrats were located in the immediate floodplain of the Swakop River and/or its tributaries, and these were predominantly sandy. In contrast, none of the Hills quadrats contained sand. The findings of previous studies indicate that soil moisture can strongly influence spatial distribution patterns of desert plant species since sand has greater water retention properties than gravel or other rocky substrates (e.g. Olsvig-Whittaker *et al.*, 1983; see also Louw & Seely, 1982; Walter, 1986). The observation that the sandy Plains species assemblage (as defined by ordination) shares greater proximity to the Swakop cluster than the Hills assemblage is consistent with this observation. However, whether or not substratum is the determining factor, and if so whether it is moisture retention which is the key feature, remains an area for future investigation.

A similar classification of plains, hills and riverine communities was also obtained by Sullivan (1993) in a recent TWINSPAN and DECORANA analysis of the vegetation of the Pro-Namib Khowarib River catchment. This similarity in results, despite markedly different survey methodologies and species composition in the study regions, suggests that this classification is a robust one. This result also lends support to Walter's (1986) assertion that desert habitats may be efficiently classified in terms of geomorphological features (see also Louw & Seely, 1982; Olsvig-Whittaker *et al.*, 1983).

In light of this, the failure to identify comparable discrete groups in the ordinations of the grid survey of low, high and very high growth form species is surprising. However, there was a discrete division of groups in the ordination of low growth forms (TWINSPAN groups E-H *vs.* I-K) which was suggestive of such a relationship. Two alternative ecological explanations can also be considered in addition to the hypothesis that these are genuinely Hills and Plains communities. First, since many of the low growth forms might be ephemerals and rainfall was patchy within the survey area, the two groups may represent areas where rain did or did not fall (or has and has not collected: Walter, 1986), respectively. Yet a comparison of the frequency of ephemerals in the two groups does not support this; ephemeral species were about equally common in both (two of 11 species in groups E-H and four of 18 in groups I-K). Second, grazing pressure from wild herbivores may have been unequally distributed in the survey area, creating distinct graze-tolerant and graze-sensitive communities (see Skarpe, 1990; Dasti & Agnew, 1994). However, an investigation of the distribution of species which showed evidence of grazing (collected from a phenological study undertaken on the basis of this survey system: Davies & Cowlshaw, unpublished) revealed approximately equal distribution between the two groups (three of 11 species in groups E-H and four of 18 in groups I-K). The failure of either of these alternative explanations to account for the observed pattern suggests that the division in the low growth form communities may reliably reflect the two communities associated with the Hills and Plains. However, further research is required to verify this.

In the case of the high growth forms, both the absence of any clear division in the ordination of this dataset and the relatively low eigenvalues suggest that the TWINSPAN classification is probably falsely imposed on what is otherwise a single community. Nevertheless, the consistent positioning of *A. senegal* and *A. mellifera* at opposite extremes of axis 1 in both the stratified survey and the high growth forms grid-based survey ordinations (Figs 7 and 9, respectively) suggests that a gradient from dry to wet conditions may nevertheless be present in the high growth forms community

(assuming that moisture is the gradient which axis 1 reflects in the ordination of the stratified survey; see above). Similarly, the grid survey of very high growth form species failed to show any pattern which related to habitat type, although a division was present which showed limited similarity to that found in the stratified survey of very high growth forms.

Why should the stratified survey so clearly identify distinct Hill and Plains communities when the grid surveys do not? The most probable reason is the size of sampling area. The stratified survey covered a total of 4 ha of the Namib region, while the grid survey spanned only 1 ha. This is why the number of very high growth form species in the former is far greater than in the latter (compare Figs 7 and 10). Yet the species-area curve for quadrats of the low and high growth form species in the grid-based survey do level off (Fig. 5). Although this plateau is considered to provide a reliable measure of the minimum area required for the definition of a community (e.g. Goldsmith *et al.*, 1986; Kent & Coker, 1992), this finding indicates that this does not guarantee that subcommunities which may be present within this community will be revealed. Indeed, these results suggest that a survey area in excess of that predicted by the species-area curve alone may be required for this task (*cf.* Campbell, 1994). This requirement may relate, at least partially, to the extreme patterns of rarity and patchiness of plant populations in this region (see above). Nevertheless, this finding stresses the importance of both the sensitivity of the species-area curve to different spatial scales (Palmer & White, 1994) and the general issue of understanding the role of spatial scale in ecological processes (May, 1994). Unfortunately, there are no simple answers, but on the basis of these results we suggest that future studies of desert communities might find it useful to consider the issue of scale particularly carefully.

We would like to thank Peter Bruce and Robin Dunbar for their help and support in this work. In addition, we are very grateful to Herta Kolberg and Coleen Mannheimer for the identification of plant species, Tim Allott and Barrie Goldsmith for advice in TWINSPAN and DECORANA methodologies, and T.A., Pat Craven, B.G., H.K., Gillian Maggs, C.M., Ben Strobach, Sian Sullivan and an anonymous referee for their helpful comments on this paper. Emmanuel de Merode and Guy Baker kindly drew the map of the study area. Climatic data for Karibib were provided by the Weather Bureau, Windhoek. This research was funded by the Natural Environment Research Council (NERC), the Central Research Fund (University of London), the Boise Fund and the Namibia Nature Foundation. We thank the Namibian Ministry of Wildlife, Conservation and Tourism and August Juchli for granting research permission in Namibia and at Tsaobis Leopard Park, respectively.

### References

- Archibold, O.W. (1995). *Ecology of World Vegetation*. London: Chapman and Hall. 510 pp.
- Bothe, H.W. (1980). *Wilsonfontein uranium joint venture prospecting grant M46/3/852*. Anglo-American Prospecting Services (Pty) Limited, Namibia. 25 pp.
- Campbell, D.G. (1994). Scale and patterns of community structure in Amazonian forests. In: Edwards, P.J., May, R.M. & Webb, N.R. (Eds), *Large-scale Ecology and Conservation Biology*, pp. 179-197. Oxford: Blackwell Scientific Publications. 375 pp.
- Dasti, A. & Agnew, A.D.Q. (1994). The vegetation of Cholistan and Thal deserts, Pakistan. *Journal of Arid Environments*, 27: 193-208.
- DeAngelis, D.L. & Waterhouse, J.C. (1987). Equilibrium and nonequilibrium concepts in ecological methods. *Ecological Monographs*, 57: 1-21.
- Fowler, N. (1986). The role of competition in plant communities in arid and semiarid regions. *Annual Review of Ecology and Systematics*, 17: 89-110.
- Gaston, K.J. (1994). *Rarity*. London: Chapman & Hall. 205 pp.
- Gauch, H.G. & Whittaker, R.H. (1981). Hierarchical classification of community data. *Journal of Ecology*, 69: 135-152.
- Giess, W. (1971). A preliminary vegetation map of South West Africa. *Dinteria*, 4: 5-14.
- Goldberg, D.E. & Turner, R.M. (1986). Vegetation change and plant demography in permanent plots in the Sonoran Desert. *Ecology*, 67: 695-712.

- Goldsmith, F.B., Harrison, C.M. & Morton, A.J. (1986). Description and analysis of vegetation. In: Moore, P.D. & Chapman, (Eds), *Methods in Plant Ecology*, pp. 437-524. Oxford: Blackwell. 589 pp.
- Günster, A. (1994). Variability in life history parameters of four serotinous plants in the Namib desert. *Vegetatio*, 114: 149-160.
- Hill, M.O. (1979a). *TWINSPAN — a FORTRAN program for averaging multivariate data in an ordered two-way table by classification of the individuals and attributes* Ithaca, NY: Cornell University.
- Hill, M.O. (1979b). *DECORANA — a FORTRAN program for detrended correspondence analysis and reciprocal averaging*. Ithaca, NY: Cornell University.
- Hill, M.O. & Gauch, H.G. (1980). Detrended correspondence analysis, an improved ordination technique. *Vegetatio*, 42: 47-58.
- Hubbell, S.P. & Foster, R.B. (1983). Diversity of canopy trees in a neotropical rain forest and implications for conservation. In: Sutton, S.L., Whitmore, T.C. & Chadwick, A.C. (Eds), *Tropical Rain Forest: Ecology and Management*, pp. 25-41. Oxford: Blackwell. 498 pp.
- Jürgens, N. (1991). A new approach to the Namib region: I. Phytogeographic subdivision. *Vegetatio*, 97: 21-38.
- Kent, M. & Ballard, J. (1988). Trends and problems in the application of classification and ordination methods in plant ecology. *Vegetatio*, 78: 109-124.
- Kent, M. & Coker, P. (1992). *Vegetation Description and Analysis: a practical approach*. London: Belhaven Press. 363 pp.
- Louw, G.N. & Seely, M.K. (1982). *Ecology of Desert Organisms*. New York: Longman. 194 pp.
- May, R.M. (1994). The effects of spatial scale on ecological questions and answers. In: Edwards, P.J., May, R.M. & Webb, N.R. (Eds), *Large-scale Ecology and Conservation Biology*, pp. 1-17. Oxford: Blackwell Scientific Publications. 375 pp.
- Merwe, van der, J.H. (1983). *National Atlas of South West Africa (Namibia)*. Cape Town: National Book Printers. 200 pp.
- Moyo, S., O'Keefe, P. & Sill, M. (1993). *The Southern African Environment*. London: Earthscan. 354 pp.
- Müller, M.A.N. (1984). *Grasses of South West Africa/Namibia*. Windhoek, Namibia: Directorate of Agriculture and Forestry. 287 pp.
- Mutangah, J.G. & Agnew, A.D.Q. (1996). Structure and diversity comparison of three dry forests at Nakuru National Park, Kenya. *African Journal of Ecology*, 34: 146-157.
- Olsvig-Whittaker, L., Shachak, M. & Yair, A. (1983). Vegetation patterns related to environmental factors in a Negev Desert watershed. *Vegetatio*, 54: 153-165.
- Palmer, M.W. & White, P.S. (1994). Scale-dependence and the species-area relationship. *American Naturalist*, 144: 717-740.
- Skarpe, C. (1990). Structure of the woody vegetation in disturbed and undisturbed arid savanna, Botswana. *Vegetatio*, 87: 11-18.
- Sullivan, S. (1993). The utilization of, and impact on, indigenous woody species at Khowarib settlement, northern Damaraland, with particular reference to those used for potentially income-generating craft activities. Unpublished MSc dissertation, University of London.
- Vasek, F.C. (1980). Creosote bush: long-lived clones in the Mojave Desert. *American Journal of Botany*, 67: 246-255.
- Yeasler, R.I. & Esler, K.J. (1990). The dynamics of a succulent karoo vegetation: a study of species association and recruitment. *Vegetatio*, 88: 103-113.
- Walter, H. (1986). The Namib Desert. In: Evenari, M., Noy-Meir, I. & Goodall, D.W. (Eds), *Ecosystems of the World: 12B Hot Deserts and Arid Shrublands*, pp. 245-282. Amsterdam: Elsevier. 451 pp.
- Ward, J.D. & Breen, C.M. (1983). Drought stress and the demise of *Acacia albida* along the lower Kusieb River, Central Namib desert: preliminary findings. *South African Journal of Science*, 79: 444-447.
- Ward, J.D., Seely, M.K. & Lancaster, N. (1983). On the antiquity of the Namib. *South African Journal of Science*, 79: 175-183.
- Wiens, J. (1984). On understanding a non-equilibrium world: myth and reality in community patterns and processes. In: Strong, D.R., Simberloff, D.R., Abele, L.G. & Thistle, A.B. (Eds), *Ecological Communities: conceptual issues and the evidence*, pp. 439-457. Princeton: Princeton University Press. 584 pp.