

D.R.F.N. : REPRINT
REFERENCE: 509
LIBRARY: WHK

Status of succulent shrubs in the southern Namib Desert, Succulent Karoo Biome

Antje Burke*

EnviroScience, PO Box 90230, Klein Windhoek, Namibia

Abstract

The ratio of dead to alive succulent shrubs as an indicator of turnover was investigated to test whether the accepted notion of rapid turnover rates and cyclic succession in the Succulent Karoo Biome are applicable in the southern Namib. Based on counts of dead and alive plants, twelve species in two habitat types were investigated. These short-term data which could not incorporate recruitment rates or changes over time, generated, however, some hypotheses. (i) Rapid turnover rates are likely not supported by all succulent plants at the Succulent Karoo Biome's northern boundary. With the exception of one species, mortality rates in succulent shrubs across a range of plant functional types were lower than reported in other parts of the biome. (ii) Sand plains appeared to support some transient species, indicating that there may be differences in vegetation dynamics between habitats. (iii) Species of different plant functional types showed no differences in ratio of dead to alive plants related to habitat. These species may have broad ecological tolerance limits and are perhaps less affected by changes in their environment. (iv) Shrubby Mesembryanthemaceae have high turnover rates and hence a short live span in the investigated area, but are longer lived than elsewhere in the Succulent Karoo Biome. As these hypotheses have implications for management and conservation of succulent species in this global biodiversity hotspot, a detailed evaluation of vegetation turnover, balancing mortality versus recruitment, should be investigated over a longer time span.

Key words: conservation, Namibia, Southern Africa, vegetation dynamics

Résumé

Le rapport de buissons succulents morts ou vivants comme indicateur de la rotation fut enquêté afin de vérifier que la notion admise des taux de rotation rapides et succession

*Correspondence: E-mail: antje.burke@enviro-science.info

cyclique dans le Biome Succulent Karoo est applicable dans le Namib méridional. Basé sur le dénombrement de plantes mortes et vivantes, douze espèces dans deux genres d'habitats furent enquêtées. Les données à court terme qui ne pouvaient pas prendre compte du taux de recrutement ni des changements au cours du temps ont néanmoins engendrées quelques hypothèses: (1) Il est probable que les taux de rotation rapide ne soient pas soutenus par toutes les plantes succulentes à la frontière septentrionale du Biome Succulent Karoo. A l'exception d'une espèce, le taux de mortalité chez les buissons succulents à travers une gamme de genres fonctionnels de plantes fut plus bas que ceux signalés dans les autres parties du Biome. (2) Des plaines de sable semblaient capable de soutenir quelques espèces de fugaces, ce qui implique des différences potentielles dans les dynamiques de la végétation entre les habitats. (3) Des espèces en provenance de différents genres fonctionnels ne montraient pas la moindre différence dans le rapport de plantes mortes aux vivantes par rapport à l'habitat. Ces espèces ont peut-être des limites d'endurance écologique extensives et sont peut-être moins touchées par les changements dans l'environnement. (4) Les *Mesembryanthemaceae* arbustifs démontrent des taux de rotation rapide et donc une durée de vie assez courte dans le zone de l'enquête, mais vivent plus longtemps qu'ailleurs dans le Biome Succulent Karoo. Etant donné que ces hypothèses ont des implications pour la gestion et la conservation des espèces succulentes dans ce point chaud de biodiversité globale, une évaluation détaillée de la rotation végétale – qui fait la balance entre la mortalité et le recrutement – devrait être enquêtée dans le long terme.

Introduction

Short life spans and resulting rapid turnover rates in succulent shrubs have been recorded in the Succulent Karoo

Biome of southern Africa (Von Willert *et al.*, 1992; Jürgens, Gotzmann & Cowling, 1999). These rapid turnover rates are predicted to be relevant throughout this biome (Cowling *et al.*, 1999). Understanding vegetation dynamics in this global biodiversity hotspot (Myers *et al.*, 2000) has implications for speciation (Cowling *et al.*, 1998) and subsequently conservation planning (Desmet *et al.*, 2002). Episodic recruitment events following good rainfall years have been observed in many parts of the Karoo, but other factors, such as local disturbances by animals and humans also play a role (Milton, Davies & Kerley, 1999). Cyclic succession has been predicted to drive vegetation dynamics in this biome (Yeaton & Esler, 1990), further supporting the notion of short life spans of plants.

The Southern Namib comprises the northern tip of the Succulent Karoo Biome and is placed at the transitional area between winter and summer rainfall in southern Africa. The succulent Karoo is expected to be most severely affected by climate change (Migley, Rutherford & Bond, 2001). Some indications already exist in declining populations of stem succulents at their margin of distribution. The effects of climate change are expected to be first noticed at this interface of the rainfall season boundary, as increased influence of one rainfall regime could gradually eliminate species adapted to the contrasting rainfall regime. In general the effects of climate change on vegetation are predicted to be species-specific (Gottfried *et al.*, 1999) and, through differential response related to the plant's physiological make-up (e.g. Schwinning & Ehleringer, 2001; Sparry & Hacke, 2002), may result in cascading effects on community structure, ecological processes and hence ecosystem functioning (Chapin *et al.*, 1998). How these changes would develop at the northern boundary of the Succulent Karoo Biome is speculation at present. The succulents present in the study area comprise a diverse mix of different phylogenetic groups and growth forms. Differential responses are hence expected.

The broader study area – the Sperrgebiet – harbours a remarkably high portion of species restricted to Namibia or the northern Succulent Karoo Biome (Burke, 2004). The area is under constant pressure from mining and exploration activities. Although environmental assessments accompany most developments in this biodiversity hotspot, the lack of information on turnover rates, natural re-establishment potential and range-sizes of endemic and rare plant species, results in environmental assessments being based on often questionable assumptions.

Decomposition rates in arid areas are extremely slow (Crawford & Gosz, 1986; West, 1991; Fernandez *et al.*, 2004). Hence dead plants decay very slowly and remain visible at their place of growth for many years (Milton *et al.*, 1999). Therefore this study used the ratio of dead to alive plants as an indication of status of succulent plant populations, which would also give some indication regarding the longevity of plants and vegetation dynamics in the study area. Although this study cannot provide the same detailed information that a long-term monitoring programme of plant population dynamics in this area would generate, it is considered an important step forward. The objective of this study is hence to develop hypotheses for plant population dynamics at the Succulent Karoo Biome's northern boundary, and thereby initiate some debate, which is hoped to result in more detailed studies in future. The ratio of dead to alive plants was investigated with regard to differences between species, habitats and phylogenetic groups.

Material and methods

The study area

Investigations were undertaken in south-west Namibia within the Sperrgebiet (Diamond Area 1) – an area with restricted access because of security measures by the diamond industry. The study area comprises a valley in the Obib Mountains, some 20 km west of Rosh Pinah (Fig. 1). Over a 16 year period rainfall at Rosh Pinah averaged 52 mm per annum, with most rains falling in June and July, although rains can occur at any time of the year. Fog frequently reaches the study area. Temperatures are moderate with the average maximum reaching 30°C in February and average minimum temperatures usually not falling below 6°C in the coldest month, August (Mendelsohn *et al.*, 2002). Deflected by the relief of the Obib Mountains, strong southerly winds prevail throughout the year. During the winter months, north-easterly bergwinds are also frequent. The habitats in this north-south trending valley include drainage lines, sand plain and quartz gravel plains as well as gravelly footslopes of the mountains. Soils are poorly developed regosols, with some sand accumulations. The main rock types are schist and quartzite interspersed with quartz veins (Geological Survey, 2000). The vegetation has been classified as succulent steppe (Giess, 1998) and is dominated by leaf-succulents, accompanied by low stem-succulent, evergreen and deciduous shrubs.

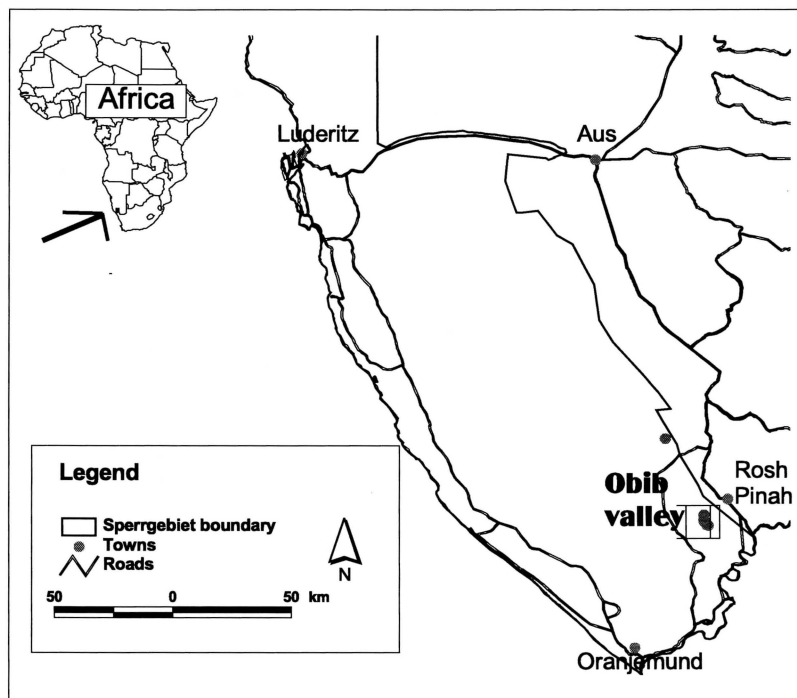


Fig 1 The study area in south-west Namibia

Field survey

In order to establish the ratio of dead to alive plants representative of the main guilds of succulent plants, plants were recorded along 2×30 to 50 m long transects during the winter growing season in the period 26 August to 5 September 2003. The length of each transect was adapted to ensure that a transect only covered one habitat type. A total of 37 transects from sand plains and quartz gravel plains was established, generating a total of 5351 individuals from twelve different species. Plant counts of alive and dead plants within these transects were restricted to species that showed active growth points, flowers or new leaves. Only rooted dead plants were included. The selected species are representative of the main guilds of perennial plants found in these habitats. Voucher specimens were lodged at the National Botanical Research Institute in Windhoek. The nomenclature follows Craven (1999). Table 1 lists the study species, their sample sizes, taxonomic and protection status and phylogenetic/growth form group.

Data analysis

The ratio of dead to alive plants was established per species and per habitat type by dividing the number of

dead individuals by the total number of individuals. The percent data were then arcsine transformed and Student's *t*-tests applied to test whether there were differences between habitats for species that occurred in the two habitat types, sand plain and quartz gravel plain (Fowler & Cohen, 1992). Single-factor analysis of variance was used to establish whether there were differences between species within habitats (Zar, 1984). The species were then grouped according to a combination of growth form and phylogenetic features. This essentially distinguished all plant families. Within the Mesembryanthemaceae (mesembs) these were further divided according to two different growth forms, either upright shrubs or compact, low and sometimes creeping succulents. The following groups were established: shrubby mesembs (Mesembryanthemaceae), tufted mesembs (Mesembryanthemaceae), euphorbs (Euphorbiaceae), bushman candles (Geraniaceae) and *zygophyllum* (Zygophyllaceae). The assignments are depicted in Table 1. Again, single-factor analysis of variance on the arcsine transformed mortality rates was used to determine whether there were differences between these growth form/phylogenetic groups (Zar, 1984). For all statistical tests a significance level of 5% was used.

Table 1 Study species, their samples sizes, phylogenetic/growth form and protection status in the Obib Valley, southern Namib

Plant species	Number of individuals		Number of transects	Family	Phylogenetic/growth form group	Status
	SP	QGP				
<i>Aridaria noctiflora</i> (L.) Schwantes subsp. <i>noctiflora</i>	46		8	Mesembryanthemaceae	Shrubby mesemb	Protected
<i>Cephalophyllum ebracteatum</i> (Pax ex Schltr. & Diels) Dinter & Schwantes	112	30	12	Mesembryanthemaceae	Tufted mesemb	Protected
<i>Cheiridopsis robusta</i> (Haw) N.E.Br.	351	688	18	Mesembryanthemaceae	Tufted mesemb	Protected
<i>Eberlanzia clausa</i> (Dinter) Schwantes	126		10	Mesembryanthemaceae	Shrubby mesemb	Protected, endemic
<i>Eberlanzia schneideriana</i> (A. Berger) H.E.K. Hartmann	23	587	18	Mesembryanthemaceae	Shrubby mesemb	Protected
<i>Euphorbia cibdela</i> N.E.Br.	78	130	29	Euphorbiaceae	Euphorb	Protected, endemic, CITES 2, red data
<i>Euphorbia mauritanica</i> L. var. <i>mauritanica</i>	30		13	Euphorbiaceae	Euphorb	CITES 2
<i>Othonna cylindrica</i> (Lam.) DC.	20		7	Asteraceae	Not included	
<i>Ruschia ruschiana</i> (Dinter) Dint. & Schwant.	36		7	Mesembryanthemaceae	Shrubby mesemb	Protected, endemic
<i>Sarcocaulon crassicaule</i> Rehm		46	6	Geraniaceae	Bushman candle	
<i>Sarcocaulon patersonii</i> (DC.) G.Don.	47		9	Geraniaceae	Bushman candle	
<i>Zygophyllum pterocaula</i> van Zyl	766	2235	24	Zygophyllaceae	Zygophyllum	

The groups are defined according to growth form and phylogeny.

Endemic, endemic to Namibia; SP, sand plain; QGP, quartz gravel plain.

Results

Species by habitat

On sand plains mortality rates per transect ranged between 0% and 75% and were variable between species and transects. *Eberlanzia clausa* and *Eberlanzia schneideriana* showed, with an average of 56% and 38% respectively, by far the highest mortality rates. Those of *Othonna cylindrica* and *Cephalophyllum ebracteatum* were the lowest. On quartz gravel plains mortality rates ranged between 0% and 59% per transect. However, average mortality rates per species were very low. Overall, mortality rates were lower on quartz gravel plains than on sand plains, averaging 15% on sand plains and 5.5% on quartz gravel plains (Table 2). These differences between habitats were not statistically supported when tested for individual species (*C. ebracteatum* $t = 2.77$, $P = 0.64$; *C. robusta* $t = 2.30$, $P = 0.9$; *E. schneideriana* $t = 2.30$, $P = 0.09$; *Euphorbia cibdela* $t = 2.06$, $P = 0.91$; *Zygophyllum pterocaula* $t = 2.13$, $P = 0.15$). The analysis of variance indicated that there were differences between species on the sand plains ($F = 4.23$,

$P < 0.0001$), but not on the quartz gravel plains ($F = 0.61$, $P = 0.69$).

Differences between phylogenetic/growth form groups

As habitat types did not affect the performance of species, but species-specific responses were found, data were combined to investigate the effect of phylogenetic/growth form features. The differences between the phylogenetic/growth form groups were significant ($F = 4.71$, $P < 0.002$). The shrubby mesembs had the highest ratio of dead to alive plants followed in decreasing order by euphorbs > zygophyllum > tufted mesembs and finally, bushman candles (Table 2).

Discussion

Although the method of a once-off assessment of dead and alive plants as an indication of population status cannot account for influences that operate over the longer time spans (e.g. drought events or other stochastic impacts), this assessment nevertheless gives a first approximation of

Table 2 Ratio and standard error of dead to alive plants in the Obib study area of Namibia's Succulent Karoo

	Ratio of dead to alive plants (%)	SE
Sand plain		
<i>A. noctiflora</i>	15.00	12.39
<i>C. ebracteatum</i>	1.92	1.47
<i>C. robusta</i>	6.35	1.64
<i>E. clausa</i>	55.88	8.91
<i>E. schneideriana</i>	37.96	15.78
<i>E. cibdela</i>	8.25	3.22
<i>E. mauritanica</i>	25.27	10.97
<i>O. cylindrica</i>	0	0
<i>R. ruschiana</i>	2.04	2.04
<i>S. patersonii</i>	4.19	2.36
<i>Z. pterocaule</i>	6.76	2.31
Quartz gravel plain		
<i>C. ebracteatum</i>	4.17	4.17
<i>C. robusta</i>	6.77	2.96
<i>E. schneideriana</i>	7.71	3.17
<i>E. cibdela</i>	7.83	3.23
<i>S. crassicaule</i>	3.33	3.33
<i>Z. pterocaule</i>	3.14	0.71

natural mortality rates of succulent shrubs in this area. Dead shrubs are expected to persist in this arid environment for several (5–10) years, hence the counts of 'standing crop' of dead and alive plants are believed to provide a good indication of the population status (Milton *et al.*, 1997). There is a possibility of differential rates of decay between species, although these appeared not to effect the present data set. For example, those plants that are expected to decay slowest, the bushman candles, did not show the highest ratio of dead to alive plants (Table 2). This would be expected, if dead plants had been accumulating more in bushman candle populations than in other populations with more rapidly decaying plants such as the tufted mesembs (personal observation).

As the ratio of dead to alive plants does not incorporate recruitment rates, nor possible differential rates of decay between species, it should not be seen as the final answer to questions relating to vegetation dynamics in this area, but as a study offering hypotheses that should be tested in future research. The discussion of the results is structured according to the hypotheses that emerged from this study.

Hypothesis 1: Overall, succulent shrubs in the Sperrgebiet have lower mortality rates than in other parts of the Succulent Karoo Biome and thus show a slower turnover.

On average projected mortality rates recorded for succulent shrubs in this study were remarkably lower than reported in the Richtersveld to the south (Jürgens *et al.*, 1999). There a mean of 60–85% was reported in four species of succulent shrubs observed over a 14 year time span (Jürgens *et al.*, 1999). In the southern Karoo 8% were reported in one woody succulent shrub, but 22–24% in shorter lived leaf succulents (Esler, Cowling & Ivey, 1992). Only one species, *E. clausa*, had a higher mean mortality rate, comparable with those in other parts of the Succulent Karoo. The other species' mortality rates were closer to those expected for other desert regions, where long-lived plants prevail (e.g. Bowers, Webb & Pierson, 1997; Cody, 2000). However, the model of cyclic succession that has been predicted for the succulent karoo (Yeaton & Esler, 1990) could still apply, although perhaps operating over longer time spans.

Hypothesis 2: Sand plains in the study area support more transient succulent perennials than quartz gravel plains. The statistical analyses related to differences between habitats and species indicated that mortality rates of plants were species-specific on sand plains, but not on quartz gravel plains, despite the fact that different plant functional types were included. This deserves a closer look. The study was only able to include six species on quartz gravel plains and hence the spread across species was not large. However, these preliminary results may suggest that sand plains support some transient species (Grime, 1998), which would show higher mortality rates and thus shorter term dynamics could be expected in some species on sand plains. The stability of the substrate and its development stage could partially explain this observed pattern. The full range of species on these two contrasting habitats would need to be investigated to make firmer predictions based on habitat type.

Hypothesis 3: Species-specific mortality rates do not differ between habitats and the investigated species may hence have a broad ecological tolerance range. No species showed statistically significant differences between habitats. This means either (i) there were indeed no differences between habitats in the investigated species or (ii) the variability in the data was too large. Variability in the data may be responsible for this pattern in *E. schneideriana*. The remaining four species showed indeed no differences, indicating that the habitat *per se* did not influence the ratio between dead to alive plants. As the physical properties of both habitats are different with regard to available water, nutrients and rooting depth, this points towards a broad

ecological tolerance limit in those species. This included compact dwarf succulents (*C. ebracteatum*, *C. robusta*) as well as a narrow-stem succulent (*E. cibdela*) and a prostrate dwarf leaf-succulent shrub (*Z. pterocaula*), indicating that this pattern was not limited to a particular plant functional type. These species may hence show resilience to changes in their environment.

Hypothesis 4: Shrubby mesembs have high turnover rates and hence a short live span in the investigated area, but are longer lived than elsewhere in the Succulent Karoo Biome. Tufted mesembs and low stem-succulent shrubs (bushman candles) showed projected slow turnover rates. Supported by statistical analysis, phylogenetic/growth form features had a marked influence on the established ratio of dead to alive plants. Shrubby mesembs showed by far the highest ratios (mean of 32%), tufted mesembs (5%) and bushman candles (4%) had the lowest. For shrubby mesembs, this pattern is in part supported by studies in other parts of the succulent karoo. In the Richtersveld to the south Jürgens *et al.* (1999) reported mortality rates of 68% for two shrubby mesembs (*Ruschia senaria* and *Stoebria beetzii*) over a 14-year observation period. Balanced with recruitment rates, this resulted in a mean life span of around 5 years for these species, which is extremely short for a desert perennial. The shrubby mesembs investigated in this study, which were represented by four different species, and not the same species as in the Richtersveld study, averaged about 32% ratio of dead to alive plants. Unfortunately no comparative figures were available for other phylogenetic/growth form groups.

Implications

The present data highlight a number of pertinent questions with major implications for management and conservation of succulent plants in the study area. If confirmed, the hypotheses put forward in this study challenge a number of established notions. (i) The assumption that succulent shrubs recover quickly and need no particular management intervention to re-establish plant cover in disturbed areas, has to be challenged. (ii) Many species of high conservation value, those that are endemic to the broader study area and thus have an extremely limited distribution in a global context, are tufted mesembs (e.g. species of the genera *Dracophilus* and *Ebracteola*). If these respond the same way as the investigated species, they appear to show very slow turnover rates, making recovery very slow, once they are

disturbed. (iii) Species-specific responses are expected to changes in climatic conditions (Gottfried *et al.*, 1999; Bakkenes *et al.*, 2002). Die-offs as a result of periodic droughts or climate change are likely to result in shifts in species composition in the vegetation of the southern Namib. In this particular case this affected species with a very limited distribution range (*E. clausa* and *E. schneideriana*). It may hence put these species at risk, if high mortality rates are the norm across their entire range and they are not balanced by appropriate levels of recruitment. In order to test the hypotheses put forward in this study, mortality rates need to be established in relation to recruitment rates and over a long time span. Only repeated sampling in permanently, fixed plots would generate these data.

Acknowledgements

The Namibian National Biodiversity Programme provided partial financial and Ambase exploration essential logistic support. I would like to thank Julien Cloete and Isaskar Uahoo for assisting with the data collection. The National Botanical Research Institute verified plant identifications and the Ministry of Environment and Tourism granted permission for this research.

References

- BAKKENES, M., ALKEMADE, J.R.M., IHLE, F., LEERMANS, R., & LATOUR, J.B. (2002) Assessing the effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. *Global Change Biol.* **8**, 390–407.
- BOWERS, J.E., WEBB, R.H., & PIERSON, E.A. (1997) Succession of desert plants on debris flow terraces, Grand Canyon, Arizona. *J. Arid Environ.* **36**, 67–86.
- BURKE, A. (2004) A preliminary account of patterns of endemism in Namibia's Sperrgebiet, succulent karoo. *J. Biogeogr.* **31**, 1613–1622.
- CHAPIN, F.S. III, OSVALDO, E.S., BURKE, I.C., GRIME, J.P., HOOPER, D.U., LAUENROTH, W.K., LOMBARD, A., MOONEY, H.A., MOSIER, A.R., NAEEM, S., PACALA, S.W., ROY, J., STEFFEN, W.L. & TILMAN, D. (1998) Ecosystem consequences of changing biodiversity. *BioScience* **48**, 45–52.
- CODY, M.L. (2000) Slow-motion population dynamics in Mojave Desert perennial plants. *J. Veg. Sci.* **11**, 351–358.
- COWLING, R.M., RUNDEL, P.W., DESMET, P.G. & ESLER, K.J. (1998) Extraordinarily high regional-scale plant diversity in southern African arid lands, subcontinental and global comparisons. *Div. Distrib.* **4**, 27–36.

- COWLING, R.M., PRESSEY, R.L., LOMBARD, A.T., DESMET, P.G. & ELLIS, A.G. (1999) From representation to persistence, requirements for a sustainable system of conservation areas in the species-rich Mediterranean climate desert of southern Africa. *Div. Distrib.* **5**, 51–71.
- CRAVEN, P. (1999) (ed) *A Checklist of Namibian Plant Species*. Southern African Botanical Diversity Network Report No. 7. SABONET, Windhoek.
- CRAWFORD, C.S. & GOSZ, J.R. (1986) Dynamics of desert resources and ecosystem processes. In: *Ecosystem Theory and Applications* (Ed. N. POLUNIN), pp. 63–88. John Wiley, New York.
- DESMET, P.G., COWLING, R.M., ELLIS, A.G. & PRESSEY, R.L. (2002) Integrating biosystematics data into conservation planning, perspectives from southern Africa's succulent Karoo. *Syst. Biol.* **51**, 317–330.
- ESLER, K.J., COWLING, R.M. & IVEY, P. (1992) Seed biology of three species of Mesembryanthema in the southern succulent Karoo. *S. Afr. J. Bot.* **58**, 343–348.
- FERNANDEZ, D., NEFF, J., BELNAP, J. & REYNOLDS, R. (2004) *Decomposition in a Desert Environment: Abiotic Regulators and Thresholds*. Abstract, Annual Meeting 2004. Ecological Society of America, Portland, Oregon.
- FOWLER, J. & COHEN, L. (1992) *Practical Statistics for Field Biology*. John Wiley and Sons, Chichester, New York.
- Geological Survey (2000) *Simplified Geological Map of Namibia*. Geological Survey of Namibia, Ministry of Mines and Energy, Windhoek.
- GIESS, W. (1998) *A Preliminary Vegetation Map of South West Africa*. Dinteria 4, 3rd revised edition. Namibia Scientific Society, Windhoek.
- GOTTFRIED, M., PAULI, H., REITER, K. & GRABHERR, G. (1999) Global change and plant diversity: a fine-scaled predictive model for changes in species distribution patterns of high mountain plants induced by global warming. *Div. Distrib.* **5**, 241–251.
- GRIME, J.P. (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J. Ecol.* **86**, 902–910.
- JÜRGENS, N., GOTZMANN, I.H. & COWLING, R.M. (1999) Remarkable medium-term dynamics of leaf-succulent Mesembryanthema (Aizoaceae) in the winter-rainfall desert of northwestern Namaqualand, South Africa. *Plant Ecol.* **142**, 87–96.
- MENDELSON, J., JARVIS, A., ROBERTS, C. & ROBERTSON, T. (2002) *Atlas of Namibia*. David Philip Publishers, Cape Town.
- MIGLEY, G., RUTHERFORD, R.M., BOND, W. (2001) *Impacts of Climate Change on Plant Diversity in South Africa*. <http://www.nbi.ac.za/climrep/>
- MILTON, S.J., YEATON, R.I., DEAN, W.R.J. & VLOK, J.H.J. (1997) Succulent Karoo. In: *Vegetation of Southern Africa* (Eds R. M. COWLING, D. M. RICHARDSON and S. M. PIERCE). Cambridge University Press, Cambridge.
- MILTON, S.J., DAVIES, R.A.G. & KERLEY, G.I.H. (1999) Population level dynamics. In: *The Karoo – Ecological Patterns and Processes* (Eds W. R. J. DEAN and S. J. MILTON). Cambridge University Press, Cambridge.
- MYERS, N., MITTERMEIER, R.A., MITTERMEIER, C.G., DA FONSECA, G.A.B. & KENT, J. (2000) Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858.
- SCHWINNING, S. & EHLERINGER, J.R. (2001) Water use trade-offs and optimal adaptations to pulse-driven arid ecosystems. *J. Ecol.* **89**, 464–480.
- SPARRY, J.S. & HACKE, U.G. (2002) Desert shrub water relations with respect to soil characteristics and plant functional type. *Funct. Ecol.* **16**, 367–378.
- VON WILLERT, D.J., ELLER, B.M., WERGER, M.J.A., BRINCKMANN, E. & IHLENFELDT, H.D. (1992) *Life Strategies of Succulents in Deserts*. Cambridge Studies in Ecology, Cambridge University Press, Cambridge.
- WEST, N.E. (1991) Nutrient cycling in soils of semiarid and arid regions. In: *Semiarid Lands and Deserts: Soil Resource and Reclamation* (Ed. J. SKUIJNS), pp. 295–332. Marcel Dekker Inc., New York.
- YEATON, R.I., ESLER, K.J. (1990) The dynamics of succulent karoo vegetation. *Vegetatio* **88**, 103–113.
- ZAR, J.H. (1984) *Biostatistical Analysis*, 2nd edn. Prentice Hall Inc., Englewood Cliffs, New Jersey.

(Manuscript accepted 5 July 2005)

