TIME SCALE.
APR - JUN 1976
MAY - SEP 1991
FOUNDATION OF NAMIBIA LIBRARY
15215

Journal of Biogeography (1998) **25**, 311–317

Floristic affinities of an inselberg archipelago in the southern Namib desert—relic of the past, centre of endemism or nothing special?

A. Burke*, N. Jürgens† and M. K. Seely* **Desert Research Foundation of Namibia, P.O. Box 20232, Windhoek, Namibia and †Universität Köln, Botanisches Institut, Gyrhofstr. 15, D-50923 Köln, Germany*

Abstract. The floral composition of an inselberg archipelago in the southern Namib desert was investigated with regard to species diversity, geographic range of the species, habitat niches, seed dispersal abilities and plant herbivore defence. Although no endemic species were found, the archipelago forms an extreme and often isolated outlier for a large number of species in their distribution area. The hypothesis is proposed that the isolated extreme habitat allowed survival of relic populations due to low immigration rate and low competition. The high proportion of species favouring long-range dispersal might explain the lack of endemic species as well as the large contribution of species at their distributional boundary.

Key words. Endemism, island biogeography, phytochorology, seed dispersal, vegetation history of the Namib Desert.

Zusammenfassung. Diese Studie untersucht die floristische Zusammensetzung einer Inselberg-flora in der südlichen Namib im Hinblick auf Diversität, geographische Verbreitung, Habitatnischen, Samenverbreitungsstrategien und Schutz gegen Herbivorie. Obwohl keine endemischen Arten vorkommen, beherbergt die Inselberg-flora dennoch eine Reihe von Arten, die hier entweder ihre äusserste Verbreitungsgrenze haben, oder Exklaven darstellen. Die isolierte, extreme Position dieser Inselbergkette in der südlichen Namib könnte niedrige Immigrationsraten und geringe Konkurrenz bedeuten, die das Überleben von Reliktpopulationen möglich machen. Die Dominanz von Arten mit Samenverbreitung durch Wind, ist möglicherweise sowohl für das Fehlen endemischer Arten, als auch für die grosse Anzahl von Arten am Rande ihrer Verbreitungsareale verantwortlich.

Stichwörter. Phytochorologie, Inselberg, Namibwüste, Reliktpopulation, Samenverbreitung.

INTRODUCTION

Relic populations of plants were often used to support theories in vegetation history (Axelrod & Raven, 1978). Extreme habitats can form a refuge for plant species during periods of adverse climatic conditions and recolonization can take place from there, following amelioration of climate. This concept was used to explain survival of arid-adapted species during wetter periods in the past, in which they retreated to arid islands within a semi-arid to mesic environment (Axelrod, 1972). Today, unfavourable climatic conditions are paralleled by grazing livestock and human activities, and many plant and animal species survive only as relic populations in areas of reduced impact from man and livestock. Isolated mountains or 'inselbergs' surrounded by an arid environment provide such refuge habitats.

Corresponding author: A. Burke, P.O. Box 34, Windhoek International Airport, Namibia.

Inselbergs are part of desert landscapes worldwide (Logan, 1964) and analysis of a number of biological inventories suggests that they often harbour species that are endemic to this particular environment or that are generally rare (Thomas & Hirnton, 1923; Gillet, 1968; Cloudsley-Thompson, 1968, 1969; Quezel, 1969). In the Namib, one of the oldest deserts of the world (Ward, Seely & Lancaster, 1983), inselbergs in the lowlands were separated from the African plateau for long periods of time. In the southern part of the Namib these inselbergs are separated by mobile dunes from similar habitats on the escarpment. Endemic animal and plant species have been found on many of the inselbergs (Newlands, 1974; Merxmüller & Buttler, 1975; Giess, 1982; Haacke, 1982). Botanical inventories, however, exist only for the most prominent one, the Brandberg (Nordenstam, 1974, 1982) which, due to its large size, forms merely a massive mountain rather than an inselberg. The most isolated inselberg archipelago, the Hauchab mountains, has not been investigated hitherto.

This archipelago is of special phytogeographical interest

© 1998 Blackwell Science Ltd

because of its position at the subcontinental boundary between the temperate and the tropical flora of southern Africa (Jürgens, 1991). Therefore we discuss the question of whether the Hauchab flora shows characteristics of both floras or whether the hypothetical refuge character has influenced the floral composition.

Unlike in other semi-arid and arid regions where livestock has been a selective force for centuries (Evenari, Shanan & Tadmor, 1982; Coley, Bryant & Chapin, 1985; Janzen, 1986), livestock has never had a great impact in this extreme and remote area. Native herbivores in this part of the Namib, such as gemsbok (*Oryx gazella* L.) and springbok (*Antidorcas marsupialis* Zimmerm.), have an episodic rather than a frequent impact on the vegetation. These unusual features could also have influenced the floristic composition. Few plant species with herbivore defence might be the result. In addition, invasive plant species are often distributed with livestock (Coblentz, 1980; Vinjevold, Bridgeford & Yeaton, 1985; Milton, Siegfried & Dean, 1990). Consequently invasive species might be absent in the inselberg vegetation.

The Hauchab mountains thus present an example of an island situation in one of the most pristine environments of the world (Huntley, 1978). The recent composition of the Hauchab flora is affected by a number of factors, such as habitat niches, seed dispersal abilities, herbivore defence, life-form spectrum and phytogeographic relations. In this study we will investigate phytogeographic relationships, seed dispersal and herbivore defence and their interaction with each other as an approach to the history of the Hauchab flora.

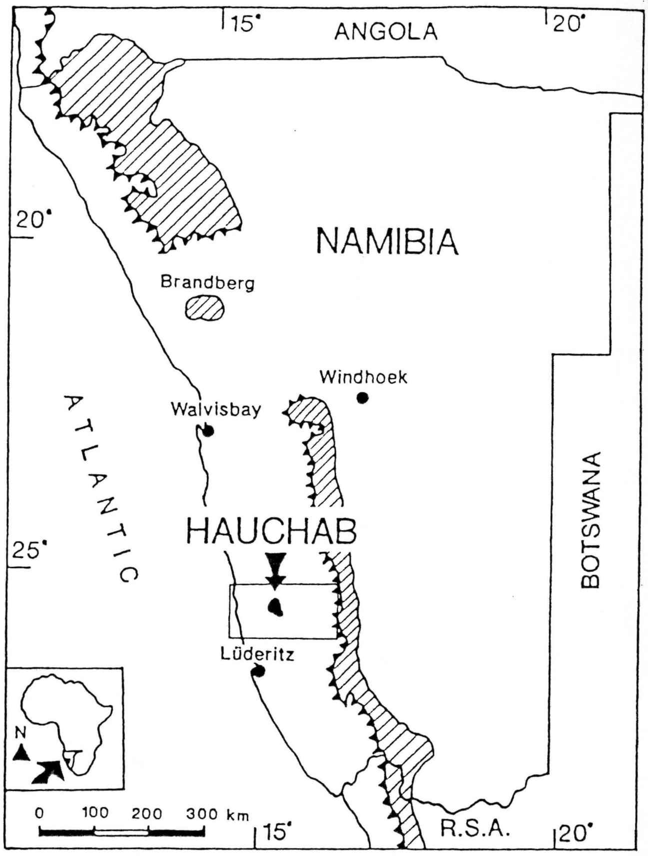

FIG. 1. Location of the study area. The hatched area indicates the Great Western Escarpment and foothills of the escarpment.

STUDY AREA

The Hauchab mountains are situated in the southern sandsea (Great Erg) of the Namib (25°20′S and 15°15′E), about 30 km from the closest inselbergs and about 50 km from the foothills of the western Escarpment of the African Plateau (Figs 1 and 2). The Hauchab mountain complex consists of two prominent outcrops, the Hauchab (1014 m above sea level) and the Uri-Hauchab (840 m above sea level) surrounded by several smaller outcrops. The mountains are composed of granitic gneiss, foliated granite, quartz porphyr and meta-sedimentary rocks (B. Hoal, pers. comm.). The landscape between the inselbergs and the escarpment is covered by sand dunes. Annual mean rainfall ranges between 20 and 50 mm (Barnard, 1964), but might be higher on the mountains due to convective effects (Gamble, 1980). Precipitation falls mainly in the summer months, but fog occurs all year round and occasionally covers the mountains. Temperatures can be extrapolated from the measurements at the Desert Research Station at Gobabeb, about 200 km north of the study area, where the monthly means range from 17.6°C to 24°C and frosts are rare (Lancaster, Lancaster & Seely, 1984). Conditions in the study area are assumed to be similar. The Hauchab has a climate typical for many parts of the Nama Karoo Region (summer rainfall regime), but with a certain influence from the winter rainfall climatic zone with its mild temperatures and high air humidity (Jürgens, 1991). The study area has not been used for farming or tourism in the past and is fenced off from the adjacent farmland at its eastern border.

METHODS

Floristic inventory

Plant collections were made on four collecting trips. Two took place after very good rains between April and June 1976, two more trips after an average rain period in May and September 1991. Species were identified and specimens housed in Herbaria at Gobabeb, Windhoek and Hamburg. A species list compiled on a farm near the escarpment (Milton, unpublished data) was incorporated for comparison. Nomenclature follows Merxmüller (1966–72), Gibbs-Russell *et al.* (1985, 1987) and recent revisions (Kolberg *et al.*, 1992).

Species classifications

The geographic distribution of species was established using the records of the reference collection of the State Herbarium of Namibia, information from the PRECIS databank of the National Herbarium (NBI) in Pretoria, the reference collection of the Desert Research Foundation of Namibia, the databank of the Mesembryanthemaceae research group in Hamburg and the databank of the Namib mapping project of the second author. Species were classified according to the distribution types in Jürgens (1994).

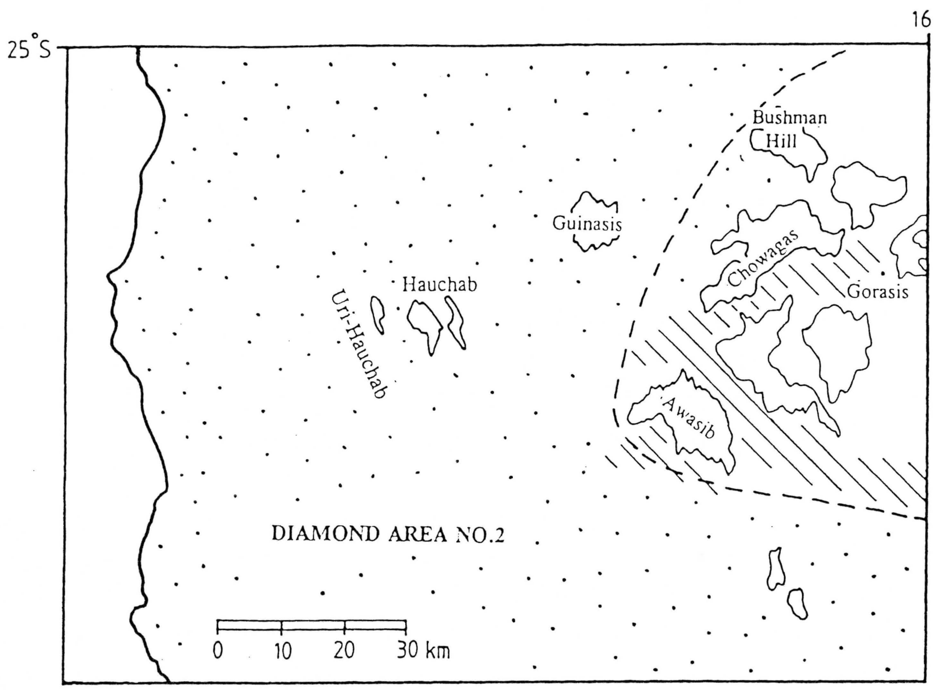

FIG. 2. Topography of the immediate surroundings of the study area (circled = mountains over 1000 m high; stippled = sand dunes; hatched = pans and plains).

Seed dispersal modes were classified (van der Pijl, 1982) after published sources (Rösch, 1977) and observations of the first author as dispersal by (a) wind, (b) animals, (c) self, (d) water and (e) no specific device. Contingency tables (Fowler & Cohen, 1992) were used to ascertain whether dispersal mode differed (a) between phytogeographic units or (b) between rainfall region (winter or summer) (2 × 5 contingency table). For this purpose species were assigned (a) to five seed dispersal modes and eight phytochorological units (5 × 8 contingency table) and (b) to two rainfall regions and five dispersal modes (2 × 5 contingency table). The phytochorological units 1, 7 and 8 resemble the winter rainfall region, while the phytochorological units 2–6 resemble the summer rainfall region.

Herbivore defence was classified into toxic species (after Watt & Breyer-Brandwijk, 1962) and spinescence.

Dispersal modes and herbivore defence of the Hauchab flora were compared to species found on a farm (Gorrasis) at the base of the escarpment.

TABLE 1. Phytochorological units represented in the Hauchab flora (number of species, percentage for $n = 71$, since there was no reliable distribution record for eleven species); last column = number of species reaching boundary of distribution area in the Hauchab. Phytochorological units 1, 7 and 8 are temperate, units 2–6 palaeotropical.

Chorological unit	Number	Percentage	
1. Succulent Karoo region (Greater Cape Flora)	14	19	10
2. Nama Karoo region: only Namib Subdomain	12	17	5
3. Nama Karoo region	27	38	2
4. Summer rainfall Karoo (African plateau)	1	1	1
5. Sudano-Zambesian region	11	16	1
6. Disjunct	1	1	1
7. Cape region (Greater Cape Flora), extended northwards	3	4	2
8. Succulent Karoo region, extended northwards	2	3	1

RESULTS

Phytogeography

The angiosperm flora of the Hauchab mountains is composed of eighty-two species, has a very inhomogeneous composition and includes members of several phytochorological units (Appendix 1). The major part of these species (fifty-two species, 72%) have areas of distribution that form part of the palaeotropical phytochorion, while nineteen species (26%) have the centre of their distribution in the temperate Cape Flora (groups 1, 7 and 8) (Table 1).

For thirty (42%) of these species the Hauchab population forms an isolated locality in an extreme position in relation to the main area of distribution. Fifteen species have their northern-most population in the Hauchab, four their north western-most, two their southern-most, one its eastern-most, two their western-most and six their south western-most population.

TABLE 2. Percentage of species of the Hauchab flora and escarpment flora (Gorrasis) with different seed dispersal syndromes ($n = 85$ at the Hauchab and 118 at Gorrasis, since species with more than one type of seed dispersal were counted several times).

Seed dispersal	Hauchab	Gorrasis
Wind	56.2	39.8
Animal	10.1	12.7
Self	13.5	16.9
Water	4.5	11.0
No specific device	10.1	11.0
Not known	5.6	8.5
Long-distance dispersal (wind and animal)	66.3	52.5
Short-distance dispersal (self, water, no device)	28.1	38.9

Seed dispersal

More than half (56.2%) of the Hauchab flora disperse their seeds by wind, while only 39.8% of the species on a farm at the escarpment (Gorrasis) distribute their seeds by wind (Table 2). Self-dispersers contribute about 13% while species with animal dispersal, and species with no specific device, contribute about 10% each to the Hauchab flora. Few species are water dispersed. On a farm situated at the base of the escarpment (Gorrasis) the contribution of dispersal syndromes other than wind was higher than at the Hauchab.

There was a significant difference in seed dispersal mode between phytochorological units ($\chi^2 = 112.4$, $P<0.01$), but not between rainfall regions ($\chi^2 = 3.33$, $P>0.05$).

Herbivore defence

The largest proportion of species had either no specific herbivore defence or their defence was not known (Hauchab: 84.2%; escarpment flora (Gorrasis): 88.4%). Known toxic species are all five members of the Euphorbiaceae, the *Salsola* species and *Ornithoglossum vulgare*. Spinescent species are *Acanthosicyos horridus*, *Cladoraphis spinosa*, *Hoodia ruschii*, *Lessertia acanthorachis* and *Solanum burchellii*.

There were more toxic species at the Hauchab (8.5%) than in the escarpment flora (Gorrasis) (2.7%), but the proportion of spinescent species was slightly lower at the Hauchab (7.3% compared to 8.9% in the escarpment flora).

DISCUSSION

Endemism

In contrast to faunal records, no endemic plant species were recorded in the Hauchab. Some reptile species, for example, are confined to that particular mountain range and are thought to be a relic of wetter periods during the glacial (Newlands, 1974; Van Zinderen-Bakker, 1975; Haacke, 1982). There are two possible explanations for the absence of plant endemism. (1) The degree of isolation of the Hauchab could have been insufficient and the high wind speeds occurring in the desert environment might have resulted in dispersal events and gene flow. This could have prevented the evolution of endemic taxa or produced a wider distribution of taxa which originally might have evolved as endemic taxa in the Hauchab. (2) Another explanation might be the possibility that endemic taxa have evolved in the past in the Hauchab which became extinct during periods of extreme climatic conditions. Time since the last event of extinction might have been too short to produce new endemic taxa.

Phytogeography

The composition of the Hauchab flora with 72% of the species belonging to the palaotropical phytochoria and 26% belonging to the temperate phytochoria seems to be in balance with its position in the Nama Karoo Region of the Palaeotropis, but near the Succulent Karoo Region of the Greater Cape Flora (Jürgens, 1997). Taxa are found in their typical habitat niches and the composition partly includes taxa characteristic of the Namib sand sea, partly taxa of rocky habitat niches, characteristic of a wide range of rocky habitats in the southern Namib.

Striking is the high proportion (42%) of taxa which have an extreme outlier of their area of distribution in the Hauchab mountains. In many cases the Hauchab population is isolated from the next occurrence of the taxon exhibiting a disjunct distribution. *Hoodia ruschii*'s closest distribution record, for example, is in the Tiras mountains 150 km south east of the Hauchab (Plowes, 1992) and the closest populations of *Rhadamanthus platyphyllus* have been recorded 200 km further north east in the Rehoboth area. With respect to the last point, a certain reservation might be necessary as the southern Namib today is floristically undercollected. More collections in future might elucidate whether or not the gap between the Hauchab populations and the main area of distribution narrows in some cases.

However, it remains noteworthy that fifteen species have their northern-most and four species their north western-most population in the Hauchab mountains. Again, two hypotheses could explain this pattern. The first hypothesis would consider a more recent expansion of the area of the Succulent Karoo Region and a preferential colonization of the Hauchab due to its poor and instable flora, part of which is often destroyed by shifting dune sand. However, this hypothesis would not be able to explain the gap between the Hauchab populations and the main areas. The second hypothesis would interpret the Hauchab populations as relic populations which were able to survive in the isolated mountain range due to a low immigration rate and resulting low competition. The strong relationship to the temperate floras in a southern direction could be explained as a result of a retreat of temperate elements. This hypothesis is in good accord with the proposed general vegetation history of this area (Van Zinderen Bakker, 1975) and with recent findings which point to an important influence of the last glaciation on the Namib flora (Jürgens, 1994).

Seed dispersal

Inefficient dispersal was suggested to be responsible for the occurrence of many rare and endemic species (Greig-Smith, 1979). Long-range dispersal is usually achieved by wind and animals (van der Pijl, 1982) and the large proportion of long-range dispersed species in the Hauchab flora might thus explain the lack of endemism in this flora. In contrast to an island situation in northern Africa, where mountain ranges with similar habitats are more than 1000 km apart (Wickens, 1976), exchanges of the Hauchab flora with the flora of the escarpment, 50 km east of the Hauchab, are likely to occur by wind dispersal. Strong easterly, southerly and westerly winds are characteristic in this region and might enable gene flow in both directions. The relationship between dispersal syndromes and phytochorological units supports the above statement. In addition, 80% of the species at their distributional boundary in the Hauchab are adapted for long-range seed dispersal.

Although conditions during the rainy season differ remarkably in winter- and summer-rainfall regions, these regions do not favour a specific type of seed dispersal. Light showers extending over a long period of time prevail in the winter rainfall region, which could promote species with self-dispersal and dispersal by rain, while thunderstorms with more intense rains prevail in the summer rainfall region; thus wind dispersal could be more advantageous here. However, other external and intrinsic factors besides the intensity of rain are important in determining the type of seed dispersal favoured by a species. Life-history characteristics and possible seed predators might play an important role (Harper, 1977).

Herbivore defence

In the Hauchab mountains, as well as in the escarpment flora, very few species showed obvious or known herbivore defence. Lacking knowledge about the toxicity of most species makes interpretation difficult. Long-term effects of herbivory are thought to play a major role in the evolution of some North American vegetation types (Campbell, 1986; Janzen, 1986) and a large proportion of the African savanna and desert plant communities (Coley *et al.*, 1985; Milton, 1991). In the study area, the long history of absence of livestock and the protection from some native herbivores might explain the low proportion of plants with herbivore defence.

Implications for management and conservation

Because of their long history of development undisturbed by human impact, the inselberg floras in the Namib are an irreplaceable genetic resource. Except for the species-rich inselberg and escarpment flora in the northern Namib, which is subjected to grazing, fuel consumption and illegal plant collections, protection of species in the southern Namib is secured at present. However, plans to develop the area for tourism exist. Careful management together with public awareness could help to conserve key areas and thus prevent extinction of rare species.

ACKNOWLEDGMENTS

Permission to work in the Namib Naukluft Park was granted by the Ministry of Environment and Tourism. We would like to thank Mike Müller, Herta Kolberg, Willi Giess and U. Meve for help with species identifications. Special thanks to S. Milton who kindly provided species lists of the escarpment flora. We acknowledge the National Botanical Institute (NBI) in Pretoria for providing grid references.

REFERENCES

Axelrod, D.I. (1972) Edaphic aridity as a factor in angiosperm evolution. *Am. Nat.* **106**, 311–320.

Axelrod, D.I. & Raven, P.H. (1978) Late and tertiary vegetation history of Africa. *Biogeography and Ecology of Southern Africa*. Vol. 1 (ed. by M.J.A. Werger), pp. 77–130. The Hague.

Barnard, W.S. (1964) Die streekspatrone van Suidwes Afrika. D.Phil. Diss., University of Stellenbosch, South Africa.

Campbell, B.M. (1986) Plant spinescence and herbivory in a nutrient poor ecosystem. *Oikos*, **47**, 168–172.

Cloudsley-Thompson, J.L. (1968) The Merkhiyat Jebels: a desert community. *Desert Biology*, Vol. I (ed. by G.W. Brown), pp. 1–20. Academic Press, New York, London.

Cloudsley-Thompson, J.L. (1969) The ecology of tropical Africa. *The world naturalist*, Weidenfeld & Nicolson.

Coblentz, B.E. (1980) Effects of feral goats on the Santa Catalina Island ecosystem. *The California Islands* (ed. by D.W. Power), pp. 167–170. Santa Barbara Museum of Natural History, Santa Barbara, California.

Coley, P.O., Bryant, J.P. & Chapin, F.S.III (1985) Resource availability and plant antiherbivore defense. *Science*, **230**, 895–899.

Evenari, M., Shanan, L. & Tadmor, N. (1982) *The Negev—the challenge of a desert*, p. 335. Harvard University Press, Cambridge.

Fowler, J. & Cohen, L. (1992) *Practical statistics for field biology*, p. 227. John Wiley & Sons, Chichester, New York.

Gamble, F.M. (1980) Rainfall in the Namib Desert. *Madoqua*, **12**, 175–180.

Gibbs-Russell, G.E., Reid, C., Van Rooy, J. & Smook, L. (1985) List of species of southern African plants, 2nd edn, part 1. *Mem. Bot. Surv. South Africa*, **51**, 1–152.

Gibbs-Russell, G.E., Welman, W.G., Retief, E., Immelman, K.L., Germishuizen, G., Pienaar, B.J., Van Wyk, M. & Nicholas, A. (1987) List of species of southern African plants, 2nd edn, part 2. *Mem. Bot. Surv. South Africa*, **56**, 1–270.

Giess, W. (1982) Zur Verbreitung des Tabaks in Südwestafrika, *Nicotinana africana* Merxm. *Dinteria*, **16**, 11–20.

Gillet, H. (1968) La vegetation du massif de l'Ennedi (Nord Tchad). *Mem. Mus. Natl. Hist. Nat.* **17B**, 206.

Greig-Smith, P. (1979) Patterns in vegetation. *J. Ecol.* **67**, 755–779.

Haacke, W.D. (1982) Distribution patterns of reptiles as indicators of geomorphological events in the Namib Desert. *Palaeoecol. S. Africa*, **15**, 225–226.

Harper, J.L. (1977) *Population biology of plants*, p. 892. Academic Press, London, New York, San Francisco.

Huntley, B. (1978) Ecosystem conservation in southern Africa. *Biogeography and Ecology of Southern Africa* (ed. by M.J.A. Werger), pp. 1335–1372. Junk, The Hague.

Janzen, D.H. (1986) Chihuahuan desert nopaleras: defaunated big mammal vegetation. *Ann. Rev. Ecol. Syst.* **17**, 595–636.

Jürgens, N. (1991) A new approach to the Namib region. I. Phytogeographic subdivision. *Vegetatio*, **97**, 21–38.

Jürgens, N. (1994) Vegetation der Namib. *Mitt. Inst. Allg. Bot. Hamburg* [in German with English summary] p. 454.

Kolberg, H., Giess, W., Müller, M.A.N. & Strohbach, B. (1992) List of Namibian plant species. *Dinteria*, **22**, 1–121.

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

Logan, R.F. (1964) The origin of the rock pediments of desert regions. *Vol. Jubilaire M.A. Lefevre*, 51–57.

Merxmüller, H. (1966–1972) Prodromus eine Flora von Südwestafrika. *Mitt. Bot. Staatssamml. München*, Vols 1–4. Cramer Verlag, Lehre.

Merxmüller, H. & Buttler, K.P. (1975) *Nicotiana* in der afrikanischen Namib—ein pflanzengeographisches und phylogenetisches Rätsel. *Mitt. Bot. Staatssamml. München*, **12**, 91–104.

Milton, S.J. (1991) Plant spinescence in arid southern Africa: does moisture mediate selection by mammals? *Oecologia (Berl.)*, **87**, 279–287.

Milton, S.J., Siegfried, W.R. & Dean, W.R.J. (1990) The distribution of epizoochoric plant species: a clue to the prehistoric use of arid Karoo rangelands by large herbivores. *J. Biogeogr.* **17**, 25–34.

Newlands, G. (1974) A description of *Hadogenes lawrence* sp. nov. (Scorpiones) with a checklist and key to the South West African species of the genus *Hadogenes*. *Madoqua*, **II**, 133–140.

Nordenstam, B. (1974) The flora of the Brandberg. *Dinteria*, **11**, 3–67.

Nordenstam, B. (1982) The Brandberg revisited. *Dinteria*, **16**, 3–5.

Plowes, D.C.H. (1992) A preliminary reassessment of the genera *Hoodia* and *Trichocaulon* (Stapeliceae: Asclepiadaceae). *Asclepios*, **56**, 5–15.

Quezel, P. (1969) Les plateaux du Dafur nord-occidental et le Jebel Gourgeil (Republique du Soudan). Etude de la flore et de la vegetation. *C.N.R.S., Dossiers de la R.C.P.*, **45**.

Rösch, M.W. (1977) Enkele plantekologiese aspekte van die Hester Malan-Natuurreservaat. Unpublished MSc. Thesis, University of Pretoria.

Thomas, O. & Hirnton, M.A.C. (1923) On the mammals obtained in Dufur by the Lynes-Loure Expedition. *Proc. Zool. Soc. Lond.* **1923**, 247–271.

van der Pijl, L. (1982) *Principles of Dispersal in Higher Plants*, p. 153. Springer Verlag, Berlin, Heidelberg, New York.

Van Zinderen Bakker, E.M. (1975) The origin and palaeoenvironment of the Namib Desert biome. *J. Biogeogr.* **2**, 65–73.

Vinjevold, R.D., Bridgeford, P. & Yeaton, D. (1985) Invasive alien plants in the Namib Naukluft Park. Invasive alien organisms in SWA/Namibia (ed. by C.J. Brown, I.A.W. MacDonald and S.E. Brown). *S. Afr. Nat. Sci. Progr. Rep.* **119**, 24–27.

Ward, J.D., Seely, M.K. & Lancaster, N. (1983) On the antiquity of the Namib. *S. Afr. J. Sci.* **79**, 175–183.

Watt, J.H. & Breyer-Brandwijk, M.G. (1962) *The medicinal and poisonous plants of Southern and Eastern Africa.* E. & S. Livingstone Ltd, Edinburgh & London.

Wickens, G.E. (1976) Speculations on long-distance dispersal and the flora of Jebel Marra, Sudan Republic. *Kew Bull.* **31**, 105–150.

APPENDIX. List of plant species encountered on and in the vicinity of the Hauchab Mountains. Sd = seed dispersal syndrome (z = animals, a = wind, s = self, h = water, no = no specific device) and dist = distribution (1 = Succulent Karoo; 2 = Namib Subdomain of the Nama-Karoo; 3 = Nama-Karoo; 4 = summer rainfall Karoo; 5 = Sudano-Zambesian; 6 = disjunct; 7 = Cape; 8 = Succulent Karoo, extended northwards; ? = no reliable distribution record). Capital letters indicate species at their boundary of distribution (NW = north west, W = west, N = north, E = east, SW = south west, S = south. * = extreme outlier).

Species	Family	sd	dist
Acanthosicyos horridus Welw. ex Hook	Cucurbitaceae	z	1
Aloe dichotoma Masson	Liliaceae	a	3
Anticharis inflata Marloth & Engel	Scrophulariaceae	?	3
Calicorema capitata (Moq.) Hook.F.	Amaranthaceae	a	3
Calicorema squarrosa (Schinz) Schinz	Amaranthaceae	a	3 NW
Centropodia glauca (Nees) T.A. Cape	Poaceae	a	3
Chamaesyce glanduligera (Pax) Koutnik	Euphorbiaceae	s	3
Chrysocoma ciliata L.	Asteraceae	a	7 W
Cladoraphis spinosa (L.F.) Phillips	Poaceae	a	1
Cleome angustifolia (Burchell) Kers	Capparaceae	s	3
Cleome sp. L.	Capparaceae	s	?
Cucumis rigidus E. Meyer ex Naudin	Cucurbitaceae	z	2 N
Dipcadi brevifolium (Thunb.) Fourc	Liliaceae	?	7 N
Dyerophytum africanum (Lam.) Kuntze	Plumbaginaceae	a	3
Eberlanzia sedoides (Dinter & Berger) Schwantes	Mesembryanthem	s,h	1 E
Ectadium virgatum var. *virgatum* E. Meyer	Periplocaceae	a	1 N
Enneapogon desvauxii Beauv.	Poaceae	a	5
Eriocephalus scariosissimus S. Moore	Asteraceae	a	3 NW
Euclea undulata var. *myrtina* Thunb.	Ebenaceae	z	5 SW
Euphorbia cf. *cibdela* N.E. Br.	Euphorbiaceae	s	?
Euphorbia gummifera Boiss.	Euphorbiaceae	s	1 N
Euphorbia lignosa Marloth	Euphorbiaceae	s	3
Euphorbia cf. *namaquensis* N.E. Br.	Euphorbiaceae	s	?
Ficus cordata Thunb.	Moraceae	z	5
Forsskoalea candida R.F.	Urticaceae	z,a	3 NW
Foveolina albida (D.C.) Kallersjö	Asteraceae	a	3
Galenia africana L.	Aizoaceae	a	7
Galenia pruinosa (L.F.) Sonder	Aizoaceae	no	1
Grielum humifusum Thunb.	Rosaceae	z	8 NW
Grielum sinuatum Lichtenst. ex Burchell	Rosaceae	z	3
Helichrysum candolleanum D.C.	Asteraceae	a	5 SW
Helichrysum gariepinum (S. Moore) Meuser	Asteraceae	a	3
Helichrysum obtusum (S. Moore) Moeser	Asteraceae	a	6 N
Helichrysum roseo-niveum Marloth & O.Hoffm.	Asteraceae	a	2 S
Heliophila trifurca Burchell ex DC.	Brassicaceae	a,h	4 N
Hermannia minimifolia M. Holzh.	Sterculiaceae	a	2
Hexacyrtis dickiana Dinter	Liliaceae	?	2
Hoodia ruschii Dinter	Asclepidiaceae	a	? *
Indigofera argyroides E. Meyer	Fabaceae	s	3
Kohautia caespitosa Schnizl.	Rubiaceae	no	5 W
Kohautia lasiocarpa Klotzsch	Rubiaceae	no	5 SW
Lessertia acanthorachis	Fabaceae	a	1 N

(Dinter) Dinter			
Lessertia marcostachya DC.	Fabaceae	a	?
Limeum argute-carinatum Warwa & Peyr.	Aizoaceae	no	5
Limeum fenestratum (Fenzl) Heimerl	Aizoaceae	a	5
Limeum viscosum (J. Gay) Fenzl	Aizoaceae	no	5 SW
Lotononis strigillosa A. Schreiber	Fabaceae	a	1 N
Monechma desertorum (Engl.) C.B. Clarke	Acanthaceae	no	3
Monsonia ignorata Merxm. & A. Schreiber	Geraniaceae	a	2
Monsonia umbellata Harvey	Geraniaceae	a	3
Myxopappus hereroensis (O.Hoffm.) T.Marl.	Asteraceae	a	1 S
Ornithoglossum vulgare B.Nord.	Liliaceae	s	5 SW
Orthanthera albida Schinz	Asclepidiaceae	a	3
Osteospermum crassifolium (O.Hoffm.) T.Norl	Asteraceae	a	1 N
Osteospermum microcarpum (Hravey) T.Nordl.	Asteraceae	a	3
Othonna furcata (Lindley) Druce	Asteraceae	a	1 N
Othonna lasiocarpa (D.C.) Schultz-Bip.	Asteraceae	a	2 N
Pelargonium crassicaule L'Herit.	Geraniaceae	a,h,s,z	1 N
Pergularia daemia var. *leiocarpa* Huber	Asclepidiaceae	a	3
Plexipus garipensis (E. Meyer) R. Fernandes	Verbenaceae	no	3
Polygala sp. L.	Polygalaceae	?	?
Pteronia polygalifolia O. Hoffm.	Asteraceae	a	2
Rhadamanthus platyphyllus B. Nord.	Liliaceae	?	? *
Salsola sp. L.	Chenopodiaceae	a	?
Senecio flavus (Dechne) Schultz-Bip.	Asteraceae	a	3
Senecio sp. L.	Asteraceae	a	?
Sesamum abbreviatum Merxm.	Pedaliaceae	a	2
Solanum burchellii Dunal	Solanaceae	z	3
Stipagrostis ciliata (Desf.) De Winter	Poaceae	a	8
Stipagrostis garubensis (Pilger) De Winter	Poaceae	a	2 N
Stipagrostis gonatostachys De Winter	Poaceae	a	2
Stipagrostis lutescens (Nees) De Winter	Poaceae	a	2
Stipagrostis subacaulis (Nees) De Winter	Poaceae	a	1
Sutera maxii Hiern	Scrophulariaceae	a	3
Sutera sessilifolia (Diels) Hiern	Scrophulariaceae	a	2
Tephrosia dregeana E. Meyer	Fabaceae	s	3
Trachyandra laxa var. *rigida* Roessl.	Liliaceae	a	5 SW
Trichodesma africanum (L.) Lehm.	Boraginaceae	no	?
Ursinea frutescens Dinter	Asteraceae	a,h	?
Zygophyllum meyeri Sonder	Zygophyllaceae	a	1 N
Zygophyllum pubescens Schinz	Zygophyllaceae	a	3
Zygophyllum simplex L.	Zygophyllaceae	no	3

BIOSKETCHES

A. Burke is a plant ecologist with a Dr.rer.nat. degree in Landscape Ecology from University of Muenster, Germany. Her research interest in arid and semi-arid regions has resulted in publications in plant population dynamics, phytosociology, patch dynamics and biogeography.

N. Juergens obtained a Dr.rer.nat. degree in Botany from the University of Hamburg, Germany. Holding a professorship at the University of Cologne, Germany, one of his main research interests is the biogeography of the southern African arid flora.

M. K. Seely is a desert ecologist with a Ph.D. from the University of California and honorary professorships at the Universities of Witwatersrand, New Mexico and Namibia. Her long-term record of research in the Namib Desert resulted in major publications concerned with animal ecology, physiology and environmental processes.