

many regards  
Wulf

# Aerial seed banks in the central Namib: distribution of serotinous plants in relation to climate and habitat

ANTJE GÜNSTER *Desert Ecological Research Unit of Namibia, P.O. Box 1592, Swakopmund 9000, Namibia*

**Abstract.** Distribution of serotinous plants in the central Namib and adjacent areas was correlated with climatic parameters (rain quantity, variability and frequency and prevailing type of precipitation) and habitat in a Binary Multiple Regression model. The desert fringe with (a) high variability of rain (60–70% of annual mean), (b) low quantities of rain (50–100 mm yr<sup>-1</sup>), and (c) prevailing precipitation type rain rather than fog, proved most conducive to serotiny. Serotinous plants were most common in habitats

where run-off accumulated, such as foothills of mountains, pans and channels, and on plains. Temporal and spatial variation of water availability, as well as intense rains and run-off, both inducing seed dispersal by water, might explain the abundance of serotinous plants at the desert fringe.

**Key words.** Climatic gradients, habitat preference, Namib Desert, seed dispersal, serotiny.

## INTRODUCTION

Seed banks are important sources of plant recruitment in desert environments (Kemp, 1989). Seeds are either dispersed and stored in the soil, called the soil seed bank, or retained above ground until seed release is triggered. The term *serotiny* has recently been introduced for this 'aerial seed bank' (Lamont, 1991). Soil seed banks have been documented in the American deserts, with emphasis on quantification and distribution of seeds in the soil (Goodall, Childs & Wiebe, 1972; Childs & Goodall, 1973; Goodall & Morgan, 1974; Nelson & Chew, 1977; Reichman, 1984; Leck, Parker & Simpson, 1989). Aerial seed banks have been described in arid and semi-arid regions (Stopp, 1958; Evenari, Shanan & Tadmor, 1982; Went, 1979), but they also exist in fire-controlled ecosystems (Smith, 1970; McMaster & Zedler, 1981; Bond, 1984; Cowling, Lamont & Pierce, 1987; Zedler, 1986) and in tropical rain forests (Van der Pijl, 1969). Bond (1984) and Zedler (1986) suggested that aerial seed banks in fire-controlled ecosystems evolved in response to frequent fires. In those systems seed release is triggered by extremely high temperatures. Other factors have to be considered in arid regions since fires do not occur. Seed release in many serotinous desert plants is triggered by moisture (Evenari *et al.*, 1982; Gutterman, 1990) and temporal and spatial variation of water availability might be of great importance. In this study, I tested the hypothesis that precipitation events and habitat types are factors which affect the distribution of serotinous desert plants. Distribution of se-

rotinous plants was recorded in the central Namib Desert and correlated with (1) type of prevailing moisture source, (2) variability of rain, (3) quantity of rain, (4) frequency of rain, and (5) habitat type.

## STUDY AREA

The study area is located in the central Namib Desert and adjacent Pro-Namib in Namibia (22°30'S to 24°00'S and 14°30'E to 16°00'E). A variety of different habitats (gravel plains, dune systems, inselbergs and escarpment) and a steep climatic gradient across a distance of 120 km provided a suitable study area (Fig. 1). Low average temperature compared to other deserts, low rainfall and regular fog events characterize the Namib Desert climate (Seely, 1978). Temperature and rain quantity increase, and humidity (fog) and variability of rain decrease from the coast (west) to the escarpment (east) (Besler, 1972; Seely & Ward, 1988). Three types of precipitation events have been identified in the Namib (Sharon, 1981; Lancaster, Lancaster & Seely, 1984): (a) infrequent storms which result in localized rainfall, (b) widespread light rain, and (c) fog. For this study four climatic belts parallel to the coast were designated: a fog-influenced belt from the coast to about 60 km inland (I), a transitional zone of about 50 km (having occasional fogs) (II), the Pro-Namib region (III), and the escarpment zone (IV) (Fig. 2). The Pro-Namib and escarpment are almost fog-free and rains are the main moisture source. Land forms and substrate determine the habitat types in the central Namib. Plains dissected by shallow drainage lines

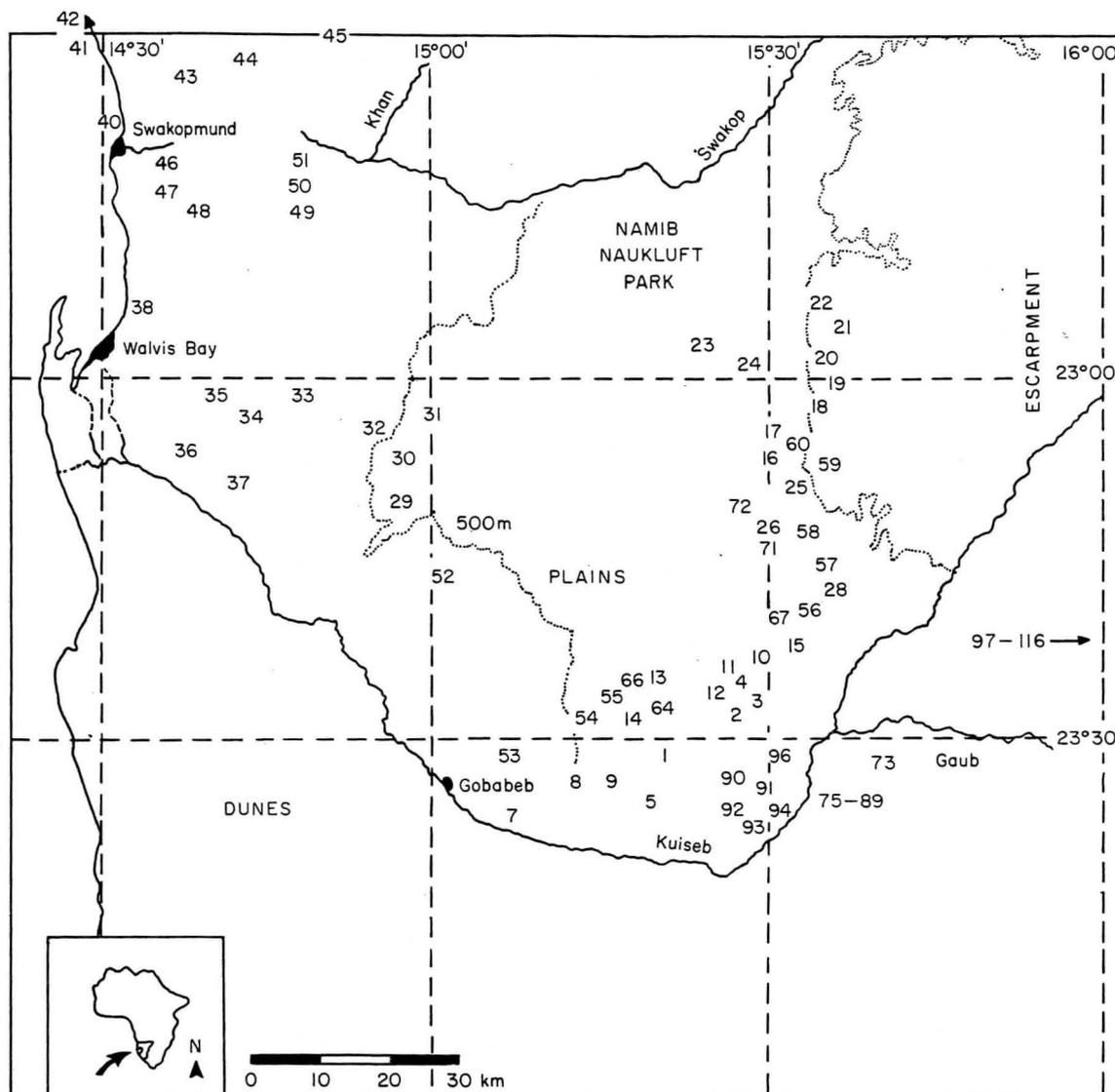


FIG. 1. Locations of transects in the study area. Each number represents a transect.

characterize the majority of the coastal area. The Kuiseb and Swakop rivers enclose the gravel plains and are the southern and northern border respectively of the study area. Gypsum crusts are commonly found in the coastal area while calcrete crusts dominate the inland plains (Martin, 1963). Mica schist is the underlying substrate in most of the study area, often covered by calcrete or gypsum crusts, quartz and other gravel, or aeolian and fluvial sandy deposits. 'Inselbergs' (isolated mountains) which mainly consist of granite (Geological Survey, 1980) are a common feature in the gravel plain area.

The vegetation in the central Namib is regularly spaced in the coastal fog zone, contracted in drainage lines on the gravel plains and regularly spaced again in the eastern part of the study area (Walter, 1986). Plant cover does usually not exceed 10% in the central Namib. Different dwarf shrub and *Acacia* species characterize the vegetation most of the year (Giess, 1981). After rain events, usually occurring between January and April, numerous annual species

add to the species spectrum, many of which are *Stipagrostis* grasses. The vegetation on the escarpment is dominated by *Acacia* trees, supplemented by shrubs and perennial grasses in the undergrowth. Here vegetation cover ranges from 15% to about 30% (pers. obs.).

## METHODS

### Vegetation survey

The fluctuations and lack of an annual plant cover in most years restricted the survey to perennial plants only, except for the annual serotinous species. Because of their above-ground seed stores, the annual serotinous plants are lignified and remain visible for years after their active period (Fig. 3a and b). The scarcity of plants required an unusual sampling method: I located line-transects in dry washes, depressions and on plains by driving on public roads through the central Namib during October 1988 to

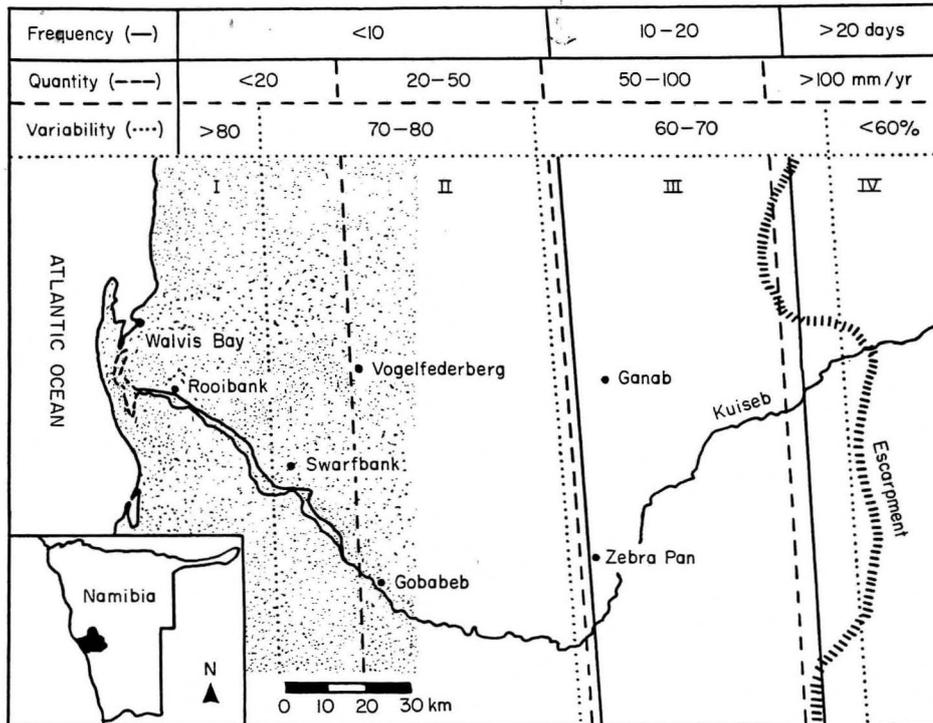


FIG. 2. Map of the study area with regions classified by quantity of rain (---), variability of rain (\*\*\*), frequency of rain (—) and prevailing precipitation type fog (shaded area) or rain (unshaded area).

November 1989. The first concentration of plants to be encountered every 5 km was selected. If those concentrations were drainage lines I laid transects out following the course of the drainage line and adjusted the width of the transect to the width of the drainage line. Transects on the plains were 5–10 m wide. Depressions with large enough diameters

were treated in the same manner as the plains. Smaller depressions were recorded in their entirety. Starting on undisturbed habitat near the road, I identified and recorded the first 100 individual plants, taller than 2 cm. In addition, length and width of the transect and a habitat description (geological nature, soil, and position) were recorded. Near

TABLE 1. Classification according to climatic parameters: mean numbers and standard errors of (a) serotinous plants per transect, (b) serotinous plants divided by species number, and (c) serotinous plants per 1 m<sup>2</sup>. (*n* = number of transects).

	<i>n</i>	(a) No.	(b) No./ species number	(c) No./m <sup>2</sup>
Prevailing type of precipitation				
Fog	24	0.9±0.9	0.2±0.2	0.003±0.003
Rain	92	28.8±3.4	5.6±1.0	0.368±0.075
Rain variability (% of annual mean)				
>80	18	0.0±0.0	0.0±0.0	0.000±0.000
71–80	24	22.7±5.9	3.7±1.0	0.351±0.090
60–70	54	37.6±4.7	7.9±1.7	0.500±0.142
<60	20	4.7±1.5	0.4±0.1	0.016±0.007
Rain quantity (mm annual mean)				
<20	18	0.1±0.1	0.0±0.0	0.000±0.000
20–50	36	30.2±5.0	5.2±1.0	0.336±0.127
51–100	42	35.4±5.6	7.8±2.1	0.474±0.112
>100	20	4.7±1.5	0.4±0.1	0.016±0.007
Rain frequency (days)				
<10	42	12.9±3.8	2.1±0.6	0.192±0.076
10–20	54	37.6±4.7	7.9±1.7	0.474±0.112
>20	20	4.7±1.5	0.4±0.1	0.016±0.007

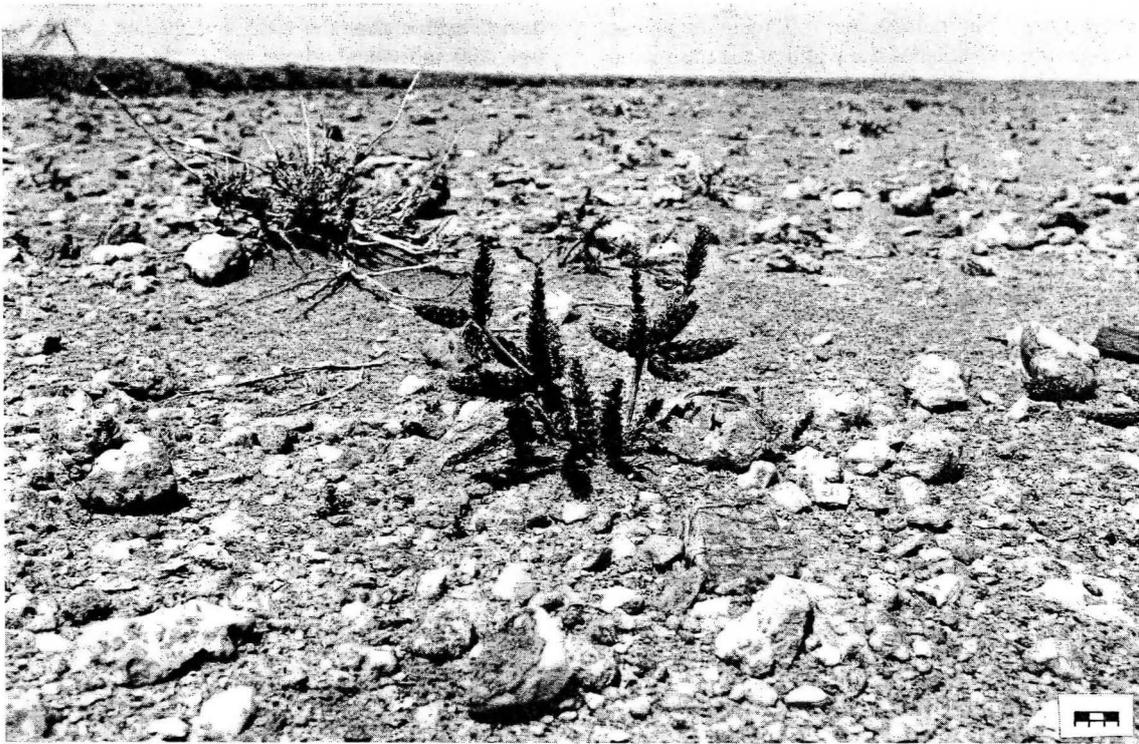


FIG.3. (Top) The serotinous *Geigeria ornativa* (Asteraceae) in the study area, 3 years after its growing period. Scale in 1 cm units. (Bottom) The serotinous *Blepharis grossa* (Acanthaceae) in the study area, 3 years after its growing period. Scale in 1 cm units.

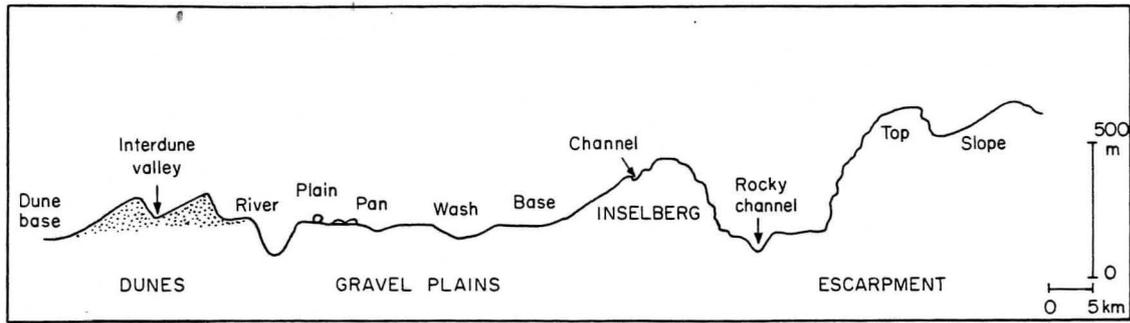


FIG.4. Schematic illustration of habitats in the study area including a hypothetical scale.

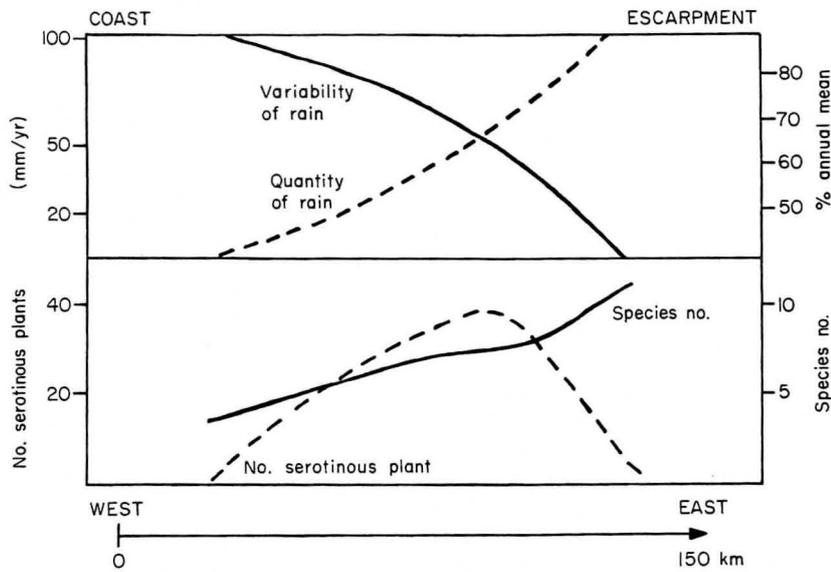


FIG.5. General trends in (a) quantity and variability of rain and (b) species number and number of serotinous plants on a west to east gradient through the central Namib.

the coast the method was modified because of the even greater scarcity of vegetation. There plants from several depressions and washes were combined until 100 plants were recorded.

Isolated mountains (inselbergs) in the study area were chosen according to accessibility. Line-transects were located and 100 plants recorded, as above, in channels,

on top and at the base of the mountains. Again, width of the transects was determined by the natural habitat. The survey was modified on the escarpment, where only serotinous species were identified and other species counted but not identified. The nomenclature follows Merxmüller (1966–71) including latest revisions. Reference specimens were deposited in the reference collec-

TABLE 2. Habitat classification: mean numbers and standard errors of (a) serotinous plants per transect, (b) serotinous plants divided by species number, and (c) serotinous plants per 1 m<sup>2</sup>. (*n* = number of transects).

	<i>n</i>	(a) No.	(b) No./ species number	(c) No./m <sup>2</sup>
Pans	4	44.0±18.4	11.6±5.9	0.17±0.10
Bases of inselbergs	5	41.0±10.5	4.1±0.9	0.31±0.09
Channels on inselbergs	6	38.8±11.8	5.9±2.0	0.92±0
Plains	9	37.2±15.4	15.2±7.3	1.03±0.57
Washes	52	26.7±4.8	4.7±1.2	0.28±0.07
Rocky channels	12	19.8±5.5	2.4±0.6	0.16±0.06
Top of escarpment ridges	6	10.7±3.9	0.9±0.3	0.04±0.02
Slope of escarpment ridges	10	2.9±1.1	0.3±0.1	0.01±0
Dune base	7	0.0±0.0	0.0±0.0	0±0
Interdune	5	0.0±0.0	0.0±0.0	0±0

tion of the Desert Ecological Research Unit. All plant species recorded on transects are listed in the Appendix, except those from the escarpment which were not identified.

### Analysis

West-east gradients of climatic factors are recognized in the study area (Lancaster *et al.*, 1984). The parameters involved are mean annual fog precipitation, mean annual rainfall, relative humidity and temperature. Rainfall variability and frequency show a west-east gradient as well (Barnard, 1964). Since temperature and relative humidity gradients are closely correlated with the occurrence of fog, they were not used in this analysis. Four climatic regions were designated (Fig. 2) based upon: (a) prevailing type of precipitation, (b) quantity of rain (annual mean), (c) variability of rain (coefficient of variation), and (d) frequency of rain (number of days/yr). Then transects were assigned to a region. Means and standard errors of number of serotinous plants were calculated for each region.

Habitat parameters were defined (Fig. 4) and transects, as above, assigned to different classes. Means and standard errors of serotinous plants were calculated for each habitat. To exclude possible effects of species number and plant density the number of serotinous plants was divided by (a) species number and (b) transect size to obtain the number of serotinous plants per 1 m<sup>2</sup>. Modified numbers were grouped by climatic and habitat parameters and means and standard errors calculated as above.

To separate the effects of dune habitat and fog as major precipitation source, means and standard errors of serotinous plants were calculated separately for dune habitats with and without fog occurrence.

The parameters that were the most significant in explaining the distribution of serotinous plants in the central Namib were investigated in a Binary Multiple Regression (BMR) (Suits, 1952; Noy-Meir, Orshan & Tadmor, 1973): The number of serotinous plants was divided into five classes (<1, 1–5, 6–20, 21–50 and >50) and a Binary Multiple Regression was carried out individually for each of the classes. Climate and habitat parameters were treated separately. Each transect was assigned a 1 for belonging and a 0 for not belonging to a specific habitat or climate group. Then a multiple stepwise regression (Sokal & Rohlf, 1981) was carried out individually for each class, and for habitat and climate parameters. The selection of parameters in the resulting regression equation showed which parameters were contributing significantly to the distribution of serotinous plants in each class.

## RESULTS

### Correlation with climate parameters

The highest mean numbers of serotinous plants were found in the region with precipitation type rain, rain variability 60–70%, quantity of rain 50–100 mm and frequency of rain 10–20 days per year (Table 1, a). The same results

were obtained when species richness and plant density were excluded (Table 1, b and c).

### Correlation with habitat

Most serotinous plants occurred in declining order in pans, at the bases of inselbergs, in channels on inselbergs, on plains and in washes (Table 2). No serotinous plants were found in dune habitats. When species richness was excluded, plains, pans, channels on inselbergs, washes, and the bases of inselbergs supported decreasing numbers of serotinous plants (Table 2, b). After excluding plant density plains, channels on inselbergs, the bases of inselbergs and pans supported decreasing numbers of serotinous plants (Table 2, c).

Illustrating the number of serotinous plants for dune and other habitats within and outside the fog zone, showed that serotinous plants did not occur in dune habitats at all (Table 3). Yet, occasionally they did occur in habitats other than dunes within the fog belt.

### Species richness and plant density

A total of eighty-seven species was recorded on ninety-six transects (plants in twenty transects from the escarpment region were excluded from the species list, since here not all species were identified). Eleven species of serotinous plants, representing 13% of all species, were encountered (see Appendix). Species richness ranged between one and sixteen species per transect. An increase of species richness from the coast (west) to the escarpment (east) was found. Transects with a total of three to six species and a range of 0–20 serotinous plants were most frequent. Plant density also increased from west to east and the number of plants per 1 m<sup>2</sup> ranged from 0.0004 to 17 plants.

### Binary multiple regression: climate parameters

The regression coefficients were significant at the 0.05 level in all cases. The class with no serotinous plants (<1) was determined by rain quantities <20 mm (Table 4). No variables were selected in the class with 1–5 serotinous plants. Rain frequencies of less than 10 days were negatively correlated with 6–20 serotinous plants. In the class with 21–50 serotinous plants, rain quantities of less than 20 mm were selected in the model. Rain frequencies of 10–20 days and rain quantities of 20–50 mm were selected in the class with more than 50 serotinous plants. Apart from the class with no serotinous plants, correlation coefficients were low (<0.35).

### Binary multiple regression: habitat parameters

Again, the regression coefficients were significant on the 0.05 level in all cases. In the classes with no serotinous plants (<1) dune base, interdune valley, and drainage lines were selected as parameters (Table 4). The correlation was positive in all three parameters, but the correlation coefficient was low in the last parameter selected (drainage lines). In the class with 1–5 serotinous plants slopes and top of mountain ridges seemed the most important parameters,

but the correlation coefficient with top of mountain ridges was below 0.5 (Table 4). Depressions were selected in the class with 6–20 serotinous plants also showing a low correlation coefficient. In the class with 21–50 serotinous plants rocky channels and the base of inselbergs were selected. Base of inselbergs had a high, rocky channels a low correlation coefficient. No parameters were selected in the class with more than 50 serotinous plants.

## DISCUSSION

At present the Pro-Namib region, with high temporal and spatial variability of water (high variability, low quantities, and low frequency of rain and prevailing moisture type rain) is the centre of distribution of serotinous plants in the central Namib and adjacent areas (Table 1 and Fig. 2). Habitats related to run-off conditions are preferred.

### Temporal variability of moisture supply

Temporal availability of water is expressed in rain frequency, variability of rain and the prevailing precipitation type. Serotinous plants occurred most frequently in regions with 50–100 mm rain, which are intermediate conditions in the study area, and with rain as a moisture source (Table 1). The coastal region with frequent fogs showed the lowest temporal variation in water available, and serotinous plants were absent there. This suggests either that high temporal variability favours seed retention or that the amount of water provided by fog is not enough to induce seed release and germination in serotinous plants.

Frequency and variability of rain are closely related to quantity of rain in deserts. Increasing quantities of rain

TABLE 3. Means and standard errors of serotinous plants per transect.

	No.	<i>n</i>
(a) In dune habitats with no fog influence	0±0	8
(b) In dune habitats with fog influence	0±0	4
(c) In habitats other than dunes with fog influence	1.05±0.99	21

result in decreasing variability and increasing frequency of rain (Barnard, 1964). The hypothetical intersection of increasing quantity and decreasing variability of rain within my scheme of classification corresponded with the highest abundance of serotinous plants in the study area (Fig. 5). The variability of moisture supply is highest here which supports the view that unpredictable rain events might have been important factors in the evolution of serotinous desert plants.

Ellner & Shmida (1981) suggested in a study in the Negev Desert, that serotiny might serve to regulate timing of germination to coincide with rain in an environment where water availability is variable and unpredictable. Since variation in water availability seems to be important for serotinous plants in the central Namib, the same explanation might be valid there.

### Large amount of water at once

Fog, which is an important moisture source for some Namib plants (Seely, De Vos & Louw, 1977; Louw & Seely, 1980; Nott & Savage, 1985), is not conducive to serotinous plants (Table 1). Precipitation from fog is higher than from rainfall in the coastal region of the Namib

TABLE 4. Regression coefficient (*r*) of the selected variables in the Binary Multiple Regression. All regression coefficients were significant at the 5% level (*n* = 116).

No. serotinous plants	Dependent variables			
	Habitat parameter		Climatic parameter	
	Variable	<i>r</i>	Variable	<i>r</i>
< 1	Dune base	0.78	Rain quantities < 20 mm	0.65
	Interdune Washes	0.78 0.23		
1–5	Slopes of ridges	0.61	No variable selected	
	Top of ridges	0.44		
6–20	Pans	0.38	Rain frequencies < 10 days	–0.13
21–50	Rocky channels	0.31	Rain quantities < 20 mm	–0.20
	Base of inselb.	0.70		
> 50	No variable selected		Rain frequencies 10–20 days	0.33
			Rain quantities 20–50 mm	0.17

Desert, but never exceeds an amount greater than 10 mm of water per fog event (DERU, unpublished). In contrast, rain showers in the study area may provide amounts of up to 80 mm at once (Lancaster *et al.*, 1984). In addition to the total amount of precipitation per year, a large amount of water at once may be an important factor for serotinous plants. This is supported by the suggestion that serotiny in desert plants is an adaptation to unpredictable rain events, seed release occurring only after a certain amount of rain fall (Ellner & Shmida, 1981; Danin, 1983).

In the regression model the absence of serotinous plants was highly correlated with rain quantities <20 mm. All other regression coefficients were low. In contrast to explaining the absence of serotinous plants, explaining their presence might be more complex than expected. Climate and habitat parameters are both important and would have to be considered together.

### Run-off

Generally, habitats accumulating water run-off, so-called 'run-on' habitats (Shmida, Evenari & Noy-Meir, 1986), were preferred by serotinous plants (Table 2). This might be explained by their means of seed dispersal which is related to water in most species. Unstable substrate might cause the lack of serotinous plants in the dunes. Plant species which are successful in unstable substrates have to be able to tolerate burial by sand for some time (Disraeli, 1984). Species tolerating burial are usually tall-growing plants such as grasses. The serotinous plants in this study are mostly growing close to the ground and might not be able to tolerate burial because of their growth form. In addition, precipitation infiltrates rapidly into sand (Hillel, 1982) and runoff in dunes is an unusual event. This supports the above statement that runoff events might be an important factor for serotinous desert plants.

Overall, the habitat type dunes has a larger impact on the distribution of serotinous plants than the prevailing precipitation type. Serotinous species are absent in dune habitats irrespective whether fog does occur or not, while occasionally they are present in the fog belt in habitats other than dunes, such as washes (Table 3). Rains are rare events in the coastal fog zone, but they do occur in some years. On such occasions seeds of serotinous plants might have been transported with run-off from inland to the coast and established few small populations.

Excluding the impact of species richness and plant density resulted in different orders of habitats with most serotinous plants, but the five highest ranked habitats remained the same in all three calculations (Table 2). This suggests that runoff-related habitats and plains were most conducive to the serotinous study plants, irrespective of interactions with other plant species.

### Other factors

Species diversity and plant density might have an impact on the distribution of serotinous plants. Transects with low species numbers were most frequently found indicating that localized distribution of plant communities with very few

species was common in the study area. Although species diversity increased towards the east, excluding its possible influence did not alter the order of climate classes with most serotinous plants (Table 1, b). Also excluding the impact of plant density did not alter the order (Table 1, c). Nevertheless, higher species diversity resulting in competition with other plants in higher rainfall regimes might explain why serotinous plants are less common in those regions.

Reasons for serotiny in an arid region have been proposed by Ellner & Shmida (1981) as a combination of several factors. In a study in the Negev Desert, they suggested that the most important factors were (a) timing and regulation of germination, (b) protection from predators, and (c) anchorage against surface run-off. Zohary (1937), who worked in the same environment, suggested that serotiny facilitated retaining the parental growth site.

Securing a once successfully occupied site for offspring is a valid argument in areas where favourable sites are not numerous, such as in arid regions. Yet competition among siblings might occur if seedlings are crowded around the parent plant. The seed-bearing structures are highly protected and this might be directed against granivores. In the Middle Eastern deserts rodents, birds and ants are recognized as seed predators (Safriel *et al.*, 1989). Similar granivores are present in the central Namib (Stuart, 1975) and some evidence exists that they harvest seeds of serotinous plants (Downs & Perrin, 1990). Other possible constraints, not recognized in the Negev, might be important in the Namib (e.g. soil properties).

On a regional scale in the central Namib run-off conditions as well as variable water availability supported serotinous plants. Studies concerned with seed dispersal and germination requirements of the serotinous species involved as well as interaction with other plants might answer questions related to the abundance of serotinous plants in certain areas and should be investigated in future studies. This study is part of a Ph.D. at the University of Munster, Germany.

### ACKNOWLEDGMENTS

I thank M. Seely for critically reading and improving the manuscript, and two anonymous referees, as well as T. Sgazzin, W. Bond and F. Daniels, for comments on an earlier draft. Financial support for this study was provided by the Desert Research Foundation of Namibia. The Ministry of Wildlife, Conservation and Tourism granted permission to work in the Namib Naukluft Park. Thanks also to the State Herbarium for help with species identifications. This study is part of a Ph.D. at the University of Munster, Germany.

### REFERENCES

- Barnard, W.S. (1964) Die streekspatrone van Suidwes-Afrika. D.Phil. dissertation, University of Stellenbosch.
- Besler, H. (1972) *Klimaverhältnisse und klimageomorphologische Zonierung der zentralen Namib (Südwestafrika)*. Stuttgarter Geographische Studien **83**, Stuttgart.

- Bond, W.J. (1984) Fire survival of Cape Proteaceae – influence of fire season and seed predators. *Vegetatio*, **56**, 65–74.
- Childs, S. & Goodall, D.W. (1973) Seed reserves of desert soils. *US/IBP Desert Biome Research Memorandum*, pp. 73–75.
- Cowling, R.M., Lamont, B.B. & Pierce, S.M. (1987) Seed bank dynamics of four co-occurring *Banksia* species. *J. Ecol.* **75**, 289–302.
- Danin, A. (1983) *Desert Vegetation of Israel and Sinai*. Cana Pub., Jerusalem.
- DERU (unpublished) Weather data of the Desert Ecological Research Unit of Namibia, Gobabeb.
- Disraeli, D.J. (1984) The effect of sand deposits on the growth and morphology of *Ammophila breviliguala*. *J. Ecol.* **72**, 145–154.
- Downs, C.T. & Perrin, R.M. (1989) An investigation of the macro- and microenvironments of four *Gerbillurus* species. *Cimbebasia*, **11**, 41–54.
- Ellner, S. & Shmida, A. (1981) Why are adaptations for long-range dispersal rare in desert plants? *Oecologia (Berl.)*, **51**, 133–144.
- Evenari, M., Shanan, L. & Tadmor, N. (1982) *The Negev – The challenge of a desert*, 2nd edn. Harvard University Press, Cambridge.
- Geological Survey (1980) Geological map of South West Africa/Namibia. Geological Survey Windhoek, Namibia.
- Giess, W. (1981) Die in der zentralen Namib von Südwestafrika/Namibia festgestellten Pflanzenarten und ihre Biotope. *Dinteria*, **15**, 13–71.
- Goodall, D.W., Childs, S. & Wiebe, H. (1972) Methodical and validation study of seed reserves in desert soils. *US/IBP Desert Research Memorandum R.M.*, pp. 72–80. Logan, Utah.
- Goodall, D.W. & Morgan, S. (1974) Seed reserves in desert soils. *US/IBP Desert Biome Research Memorandum R.M.*, pp. 74–116. Logan, Utah.
- Gutterman, Y. (1990) Seed dispersal by rain (ombrohydrochory) in some of the flowering desert plants in the Israel and Sinai Peninsula. *Mitt. Inst. Bot. Hamburg*, **23b**, 841–552.
- Hillel, D. (1982) *Negev – land, water and life in a desert environment*. Praeger Publ., New York.
- Kemp, P.R. (1989) Seed banks and vegetation processes in deserts. *Ecology of soil seed banks* (ed. by M. A. Leck, V. T. Parker and R. L. Simpson), pp. 257–281. Academic Press, New York.
- Lamont, B. (1991) Canopy seed storage and release – what's in a name? *Oikos*, **60**, 266–268.
- Lancaster, J., Lancaster, N. & Seely, M.K. (1984) Climate of the central Namib Desert. *Madoqua*, **14**, 5–61.
- Leck, M.A., Parker, V.T. & Simpson, R.L. (1989) *Ecology of soil seed banks*. Academic Press, New York.
- Louw, G.N. & Seely, M.K. (1980) Exploitation of fog water by a perennial Namib dune grass *Stipagrostis sabulicola*. *S. Afr. J. Sci.* **76**, 38–39.
- Martin, H. (1963) A suggested theory for the origin and brief description of some gypsum deposits of South West Africa. *Trans. Geol. Surv. S. Afr.* **66**, 345–351.
- McMaster, G.S. & Zedler, P.H. (1981) Delayed seed dispersal in *Pinus torreyana* (Torrey Pine). *Oecologia (Berl.)*, **51**, 62–66.
- Merxmüller, H. (1966–72) *Prodromus einer Flora von Südwestafrika*. Bot. Staatssamml. München, Vols 1–4.
- Nelson, J.F. & Chew, R.M. (1977) Factors affecting seed reserves in the soil of a Mojave Desert ecosystem, Rock Valley, Nye Country, Nevada. *Am. Midl. Nat.* **97**, 300–320.
- Nott, K. & Savage, M.J. (1985) Variation in seasonal and diurnal leaf water potential of a Namib dune succulent. *Madoqua*, **14**, 177–179.
- Noy-Meir, I., Orshan, G. & Tadmor, N.H. (1973) Multivariate analysis of desert vegetation. III. The relation of vegetation units to habitat classes. *Israel J. Bot.* **22**, 239–257.
- Reichman, O.J. (1984) Spatial variation of seed distributions in Sonoran Desert Soils. *J. Biogeogr.* **11**, 1–11.
- Safriel, U.N., Ayal, Y., Kotler, B.P., Lubin, Y., Olsvig-Whittaker, L. & Pinshow, B. (1989) What's special about desert ecology? *J. Arid Env.* **17**, 125–130.
- Seely, M.K. (1978) The Namib Dune Desert: an unusual ecosystem. *J. Arid Env.* **1**, 117–128.
- Seely, M.K., De Vos, M.P. & Louw, G.N. (1977) Fog imbibition, satellite fauna and unusual leaf structure in a Namib Desert dune plant, *Trianthema hereroensis*. *S. Afr. J. Sci.* **73**, 169–172.
- Seely, M.K. & Ward, J.D. (1988) The Namib Desert. Long-term data series relating to southern Africa's renewable natural resources. *S. Afr. Nat. Sci. Progr. Rep.* **157**, 268–279.
- Sharon, D. (1981) The distribution in space of local rainfall in the Namib Desert. *J. Climatol.* **1**, 69–75.
- Shmida, A., Evenari, M. & Noy-Meir, I. (1986) Hot desert ecosystems: an integrated view. *Ecosystems of the world*, Vol. 12B (ed. by M. Evenari, I. Noy-Meir and D. W. Goodall), pp. 379–387. Elsevier, Amsterdam.
- Smith, C.C. (1970) The coevolution of pine squirrels (*Tamiasciurus*) and conifers. *Ecol. Monogr.* **40**, 349–371.
- Sokal, R.R. & Rohlf, F.J. (1981) *Biometry*. W. H. Freeman and Company, New York.
- Stopp, K. (1958) *Die verbreitungshemmenden Einrichtungen der südafrikanischen Flora*. Bot. Studies 8, Jena.
- Stuart, C.T. (1975) Preliminary notes on the mammals of the Namib Desert Park. *Madoqua*, **II**, 5–68.
- Suits, D. (1952) Use of binary variables in regression equations. *J. Am. Stat. Assoc.* **52**, 548–551.
- Van der Pijl, L. (1969) *Principles of Dispersal in Higher Plants*. Springer, Berlin.
- Walter, H. (1986) The Namib Desert. *Ecosystems of the world*, Vol. 12B (ed. by M. Evenari, I. Noy-Meir and D. W. Goodall), pp. 245–282. Elsevier, Amsterdam.
- Went, F.W. (1979) Germination and seedling behavior of desert plants. *Arid land ecosystems, Vol. I* (ed. by D. W. Goodall and P. A. Perry), pp. 477–490. Cambridge.
- Zedler, P.H. (1986) Closed-cone conifers of the chaparral. *Fremontia*, **14**, 14–17.
- Zohary, M. (1937) *Die verbreitungsökologischen Verhältnisse der Pflanzen Palästinas. I. Die antitelechorischen Erscheinungen*. Beih. Bot. Centralbl., Abt. A, **46**(1), 1.

## APPENDIX

Plant species recorded on vegetation transects. Serotinous plants are marked with an asterisk. The nomenclature follows Merxmüller (1966–72) including latest revisions (State Herbarium of Namibia).

Species	Family
<i>Abuliton pycnodon</i>	Malvaceae
<i>Acacia reficiens</i>	Fabaceae
<i>Adenolobus garipensis</i>	Fabaceae
<i>Adenolobus pechuelii</i>	Fabaceae
<i>Aizoanthemum galenioides</i>	Aizoaceae
<i>Aptosimum arenarium</i>	Scrophulariaceae *
<i>Aptosimum spinescens</i>	Scrophulariaceae *
<i>Arthroaerua leubnitziae</i>	Amaranthaceae
<i>Asclepias buchenaviana</i>	Asclepiadaceae
<i>Barleria merxmülleri</i>	Acanthaceae
<i>Berkheya spinosissima</i>	Asteraceae

<i>Blepharis bossii</i>	Acanthaceae	*	<i>Maerua schinzii</i>	Capparaceae
<i>Blepharis grossa</i>	Acanthaceae	*	<i>Maytenus heterophylla</i>	Celastraceae
<i>Blepharis obmitrata</i>	Acanthaceae	*	<i>Mesembryanthemum crystallinum</i>	Mesembryanthemaceae
<i>Blepharis pruinosa</i>	Acanthaceae	*	<i>Monechma arenicola</i>	Acanthaceae
<i>Boscia foetida</i>	Capparaceae		<i>Moringa ovalifolia</i>	Moringaceae
<i>Brownanthus kunzei</i>	Mesembryanthemaceae		<i>Orthanthera albida</i>	Asclepiadaceae
<i>Calicorema capitata</i>	Amaranthaceae		<i>Osteospermum microcarpum</i>	Asteraceae
<i>Calostephane marlothiana</i>	Asteraceae		<i>Otopotera buchellii</i>	Fabaceae
<i>Citrullus ecirrhosus</i>	Cucurbitaceae		<i>Pechuel-Loeschia leubnitziae</i>	Asteraceae
<i>Cladoraphis spinosa</i>	Poaceae		<i>Pegolettia senegalensis</i>	Asteraceae
<i>Cleome foliosa</i>	Capparaceae		<i>Pergularia daemia</i>	Asclepiadaceae
<i>Codon royenii</i>	Hydrophyllaceae		<i>Petalidium setosum</i>	Acanthaceae
<i>Commicarpus squarrosus</i>	Nyctaginaceae		<i>Petalidium variabile</i>	Acanthaceae
<i>Commiphora glaucescens</i>	Burseraceae		<i>Phaeoptilum spinosum</i>	Nyctaginaceae
<i>Commiphora saxicola</i>	Burseraceae		<i>Plexipus garipense</i>	Verbenaceae
<i>Cucumella aspera</i>	Cucurbitaceae		<i>Protasparagus denudatus</i>	Liliaceae
<i>Curroria decidua</i>	Periplocaceae		<i>Psilocaulon salicornioides</i>	Mesembryanthemaceae
<i>Drosanthemum paxianum</i>	Mesembryanthemaceae		<i>Ptychobium biflorum</i>	Fabaceae
<i>Dyerophytum africanum</i>	Plumbaginaceae		<i>Rogeria longiflora</i>	Pedaliaceae
<i>Chamaesyce glanduligera</i>	Euphorbiaceae		<i>Ruellia diversifolia</i>	Acanthaceae
<i>Euphorbia virosa</i>	Euphorbiaceae		<i>Salsola nollothensis</i>	Chenopodiaceae
<i>Fagonia isotricha</i>	Zygophyllaceae		<i>Salsola tuberculata</i>	Chenopodiaceae
<i>Forsskoalea candida</i>	Urticaceae		<i>Senecia alliarifolius</i>	Asteraceae
<i>Galenia africana</i>	Aizoaceae		<i>Senecio engleranus</i>	Asteraceae
<i>Galenia procumbens</i>	Aizoaceae		<i>Sesamum capense</i>	Pedaliaceae
<i>Geigeria alata</i>	Asteraceae	*	<i>Sesuvium sesuvioides</i>	Aizoaceae
<i>Geigeria ornativa</i>	Asteraceae	*	<i>Solanum namaquensis</i>	Solanaceae
<i>Hermannia abrotanoides</i>	Sterculiaceae		<i>Stipagrostis lutescens</i>	Poaceae
<i>Heliotropium supinum</i>	Boraginaceae		<i>Stipagrostis sabulicola</i>	Poaceae
<i>Helichrysum tomentosulum</i>	Asteraceae		<i>Sutera canescens</i>	Scrophulariaceae
<i>Hermbstaedia argenteiformis</i>	Amaranthaceae		<i>Sutera maxii</i>	Scrophulariaceae
<i>Hermbstaedia spathulifolia</i>	Amaranthaceae		<i>Tephrosia dregeana</i>	Fabaceae
<i>Hirpicium gazanioides</i>	Asteraceae		<i>Trichodesma africanum</i>	Boraginaceae
<i>Indigofera sp.</i>	Fabaceae		<i>Tribulus zeyheri</i>	Zygophyllaceae
<i>Kissenia capensis</i>	Loasaceae		<i>Ziziphus mucronata</i>	Rhamnaceae
<i>Kohautia ramossissima</i>	Rubiaceae		<i>Zygophyllum clavatum</i>	Zygophyllaceae
<i>Limeum argute-carinatum</i>	Molluginaceae		<i>Zygophyllum cylindrifolium</i>	Zygophyllaceae
<i>Lycium tetrandum</i>	Solanaceae		<i>Zygophyllum stapffii</i>	Zygophyllaceae