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Abstract entered

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Precipitation and biomass changes in the Namib Desert dune ecosystem

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Parts of the Namib Desert receive 19 mm of rain and 35 mm of fog precipitation on average during a year in amounts insufficient for plant germination and establishment. Major rainfall events which permit plant germination occur so infrequently that comparatively little is known about the relationship between biomass production and precipitation and the fate of biomass in this hyper-arid environment. Plant and invertebrate biomass sampling has previously been conducted in 1975 and 1976 preceding and following an exceptionally wet period when over 80 mm of rain fell in a few weeks. We used the same study area and equivalent methods to repeat the sampling in 1985 and 1991 and examine the changes in plant and invertebrate biomass in relation to rain and fog records. The decline and distribution of biomass was different from that predicted by the previous study, most probably because the continued growth of perennial plants on the dune slopes was not fully anticipated. *Stipogrostis sabulicola* and *Trianthema hereroensis* can imbibe fog and continued to contribute biomass to the system while nothing else could grow; in addition, the presence and structure of these plants probably trapped detritus which otherwise would have been blown between the dune slip faces and interdunes.

Keywords: biomass fluctuations; Namib Desert; rainfall; fog

Introduction

Productivity over time in desert regions is largely limited by the amount and the predictability of precipitation. We examined changes in the plant and animal biomass at a study site in the central Namib Desert in relation to fog and rainfall over a 16-year period.

In general, the drier the desert, the greater the unpredictability of rainfall (MacMahon, 1981; Evenari, 1985). The central Namib Desert is known to be one of the driest regions in the world and its climate is influenced by the cold Benguela current on the west coast and the El Nino/Southern Oscillation (Nicholls & Wong,

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1990). The study region receives an average rainfall of only 19 mm per annum (Meteorological Bureau records 1962–91). However, the rainfall is supplemented by fog and the fog precipitation averages 37 mm per annum (Meteorological Bureau records 1966–1991, Gobabeb). Fog is an important moisture source for this region contributing twice as much moisture as rainfall with a third of the variability (Robinson & Seely, 1980; Pietruszka & Seely, 1985). This has led to the evolution of endemic fauna and flora which use rainfall as well as fog as a moisture source (Hamilton & Seely, 1976; Seely & Hamilton, 1976; Seeley, 1978, 1979; Louw & Seely, 1980; Seeley *et al.*, 1983).

Seely & Louw (1980) conducted biomass sampling in a central Namib dune ecosystem in 1975, at the end of a dry period that had apparently extended since 1934 (Meteorological Bureau records, South-West African Administration), and again following a sporadic high rainfall event which occurred in early 1976. They estimated that the biomass increased from 3 $g.m^{-2}$ to 26 $g.m^{-2}$ following the germination and establishment of perennial and ephemeral plants and formulated a model to describe the long-term biomass changes in the Namib in accordance with precipitation (Louw & Seely, 1982). The model suggested that the biomass of the three main dune habitats, interdune, dune slope and slipface, varied differently over time. This paper tests the accuracy of this model in the light of further changes in the plant and animal biomass at the location used by Seely & Louw (1980).

Methods

Study area

The climate of the Namib Desert dune system changes from a predominantly winter rainfall in the south to summer dominating pattern in the north. Fog precipitation is greatest near the coast, decreasing further inland, while rainfall shows the opposite trend and increases markedly from west to east (Pietruszka & Seely, 1985). The study area was located near Gobabeb (23 34'S, 15 03'E) in the driest portion of the central Namib. Precipitation records indicated that most rain fell between January and April, whereas fog precipitation was greatest in June and July (Lancaster *et al.*, 1984).

Within the dune ecosystem there were the three main habitats: interdune valley, dune slopes and slipfaces. At the study site, the dunes were spaced about 2 km apart running predominantly north–south. The interdune valleys were relatively flat with a lightly consolidated sandstone and gravel substrate. The dune slopes rose to a height of 100 m above the interdune valleys and consisted of loosely consolidated sand. Windward slopes were steeper and shorter than leeward slopes. The slipfaces were steep sandy faces (32°) of loosely packed and well aerated sand. They were located on either side of the dune and at various locations on the slope. Wind blown detritus collected at the base of the slipfaces because of the vortex created by the steepness of the face. The physiography for this region has been described in greater detail by Seely & Louw (1980) and Robinson & Seely (1980).

The perennial species *Stipogrostis sabulicola, Trianthema hereroensis* and the nara melon, *Acanthosicyos horridus*, occurred on the dune base and lower slopes. Facultatively ephemeral plant species including *Centropodia glauca* (= *Asthenatherum glaucum*), *Cladoraphis spinosa* (= *Eragrostis spinosa*), *S. gonatostachys* and *Monsonia ignorata* have been recorded on the slopes and interdunes following rain (Seely & Louw, 1980).

Analysis of precipitation

The precipitation records from Gobabeb (1962–1991) were examined using monthly and annual rainfall, fog and precipitation values. The mean, coefficient of variation (CV) and the cumulative deviation from the mean (CDM) were calculated (Sutherland *et al.*, 1991) for the above data. The CDM was plotted to determine the cumulative high and low periods of rain, fog and total precipitation. Annual precipitation was calculated for rainfall years (July–June). Periods when more than 10 mm or 20 mm of rain fell within a 5-day period were noted to indicate when germination of ephemerals and perennials may have occurred.

Biomass estimates

In May 1985 and November 1991 plant and animal biomass was sampled within the same study area and using similar procedures as Seely & Louw (1980). The same three habitats were sampled; interdune valleys, dune slopes and slipfaces which comprise approximately 55%, 44% and 1% of the dune system, respectively (Seely & Louw, 1980). Vegetation biomass was sampled at five sites for each of the three main habitats. At each site, a 20 × 20 m square was measured. A 0·5 × 0·5 m quadrat was placed at each corner and in the centre of the square. At each quadrat, all plant and animal matter was collected from the surface and then the substrate was excavated to a depth of 200 mm. On the slipfaces, two excavations were made at the base of the slipface, two on the crest, and one in the middle. All excavated sand was passed through a sieve of 1·0 mm mesh to collect the plant and animal material present. Vegetation was defined as plant remains plus windblown detritus and similarly, animal material included living and dead animal matter. The material collected was then dried for 48 h at 70 °C and immediately weighed to obtain dry weight of the biomass.

A second sampling technique estimated the biomass of the two most common perennial plants, *Trianthema hereroensis* and *Stipogrostis sabulicola*. In the 1985 sample, five individuals of *S. sabulicola* and *T. hereroensis* were entirely excavated. Biomass per area was obtained by dividing the mass of plant material by the area of the plant. In 1991, a 0·25 m^2 quadrat sample was taken from 10 plants to avoid destruction of the whole plant.

The contribution of the plants to total vegetative biomass was estimated by multiplying the average plant dry weight g.m^{-2} by the average size of the plants and the number of plants per area of slope. The average plant size was obtained from a sample of 40 randomly selected plants of each species. The breadth and width of each plant was measured and the area calculated by multiplying these values. The density of both dead and alive individuals of each species was obtained from six transects spaced at between 2 and 4 km apart and each 1 km long and 190 m wide. The values for plant size and density were not recorded in 1985; instead data from Seely (1990) were used to estimate perennial plant abundance and size for the 1985 sample.

Animal biomass was estimated by recording the abundance of invertebrates occurring in each quadrat and multiplying each individual by representative dry body mass. Voucher specimens were used to determine dry body mass of the species collected. The additional transect and observational sample methods employed by Seely & Louw (1980) to estimate animal biomass were not used during the 1985 and 1991 census.

Results

Precipitation trend

The Gobabeb records 1962–1991 gave a mean annual rainfall of 19 mm, with a range from 0–107 mm. Mean annual fog was 37 mm with a range of 14–68 mm, and annual precipitation was 56 mm with a range of 18–127 mm. The coefficients of variation were 113% for rainfall, 37% for fog and 45% for precipitation. These coefficients were similar to those calculated by Pietruszka & Seely (1985).

Because graphs of the cumulative deviation from the mean (CDM) showed similar trends for monthly and annual precipitation, only annual data are presented. The CDM rainfall shown in Fig. 1 indicates that the period from 1962/63 to 1974/5 was much drier than average. Rainfall between 1975/6 and 1978/9 was extremely high but since then there have been below average falls resulting in a steady decline in the cumulative total.

In the 14 years of records prior to 1976, six 10-mm events were recorded but there was no rainfall event greater than 20 mm. Since 1976, two 10-mm events occurred prior to 1985 and three between 1985 and 1991. Two events in excess of 20 mm have occurred; in 1976 and 1978.

The CDM of fog precipitation (since 1962/3) is shown in Fig. 2. Generally this precipitation follows an inverse pattern to the rainfall with very low averages experienced from 1974/5 to 1985/86 and a marked increase thereafter.

Figure 3 illustrates the pattern of the total precipitation. The combination of fog and rain as a precipitation source indicates long periods of precipitation deficit, for example 1970–75 and 1982–85. The deviations from the calculated mean were reduced when the two moisture sources are combined however, one moisture source cannot be considered to compensate for the other.

Vegetation biomass

The biomass estimates for vegetation collected from the quadrats are presented in Table 1. Biomass was unevenly distributed in the desert dune system above- and below-ground and over time and space. Before the big rains in 1976, biomass values were very low and most was found below-ground and associated with interdune areas.

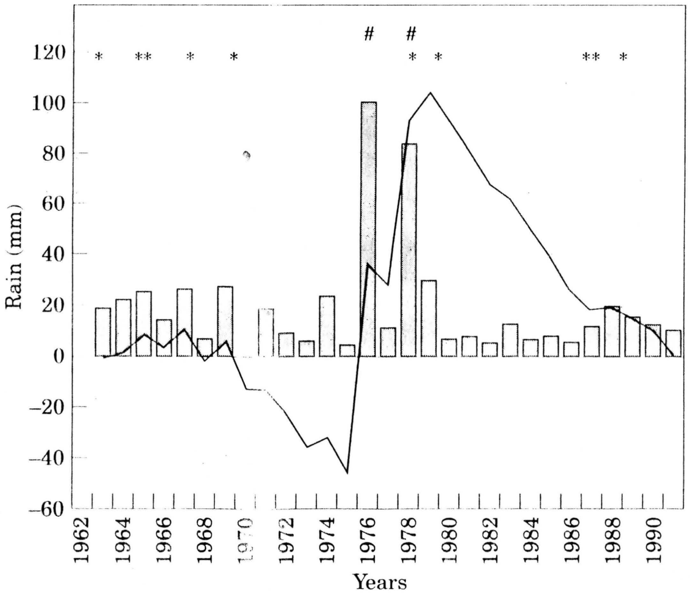

Figure 1. Annual rainfall for Gobabeb (☐) and cumulative deviation (CDM) from the mean (——). * indicates > 10 mm of rain in a 5-day period and # indicates > 20 mm.

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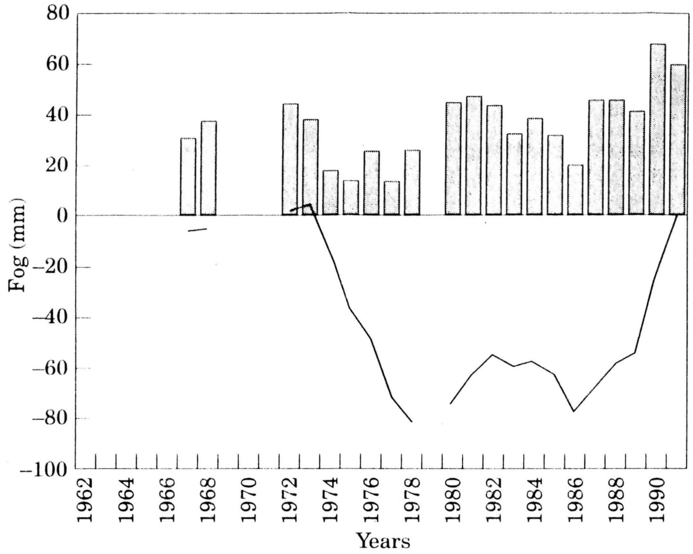

Figure 2. Annual fog for Gobabeb (☐) and cumulative deviation (CDM) from the mean (—). No fog data for 1962–1966, 1969–1971 and 1979.

Following the rain, there was a massive increase in biomass in each habitat; the biomass was recorded primarily above-ground and a large amount was being trapped on the slip faces. In 1985, detrital biomass was still most abundant on the slipfaces and least abundant on the dune slopes; much of the biomass was still located above-ground. Sampling in 1991 revealed that the majority of detrital biomass was now present below-ground and it was located predominantly on the dune slope habitat. The amount of vegetative biomass on the dune slope is further increased when the estimates for the perennial plants are added to the total.

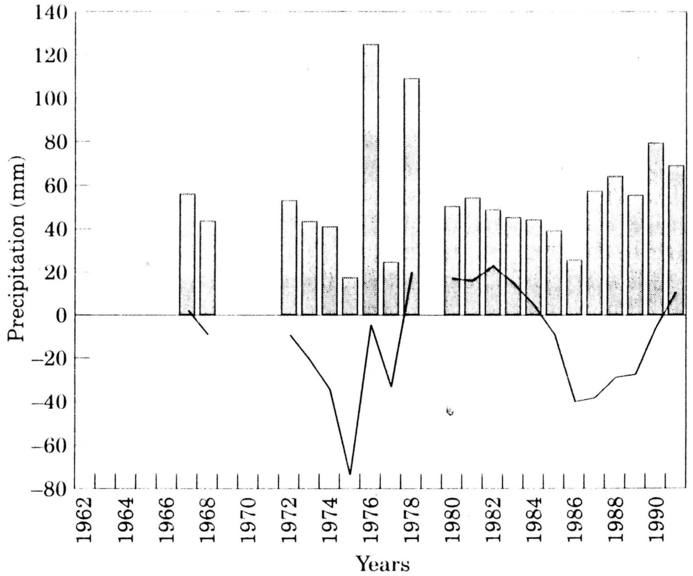

Figure 3. Annual precipitation for Gobabeb (☐) and cumulative deviation (CDM) from the mean (—). No fog data for 1962–1966, 1969–1971 and 1979.

Table 1. *Vegetative biomass (g.m^{-2}) obtained for three habitat types during four sampling periods (excluding perennial plants) on and below the surface of the habitats*

	Vegetative biomass (g.m^{-2})													
	1975		1976		1985				1991					
Habitat	M	SE	M	SE	M	SE	n	Range	M	SE	n	Range		
Interdune valley														
Surface	4·4	1·4	23·2	3·0	12·5	5·7	24	0·1–141·7	0·7	0·4	25	0–9·3		
Subsurface	4·9	1·2	2·0	0·3	4·5	0·7	25	0·5–13·8	1·6	0·5	25	0–10·7		
Total	9·3	—	25·2	—	17·0	5·9	24	0·8–147·9	2·3	0·8	25	0–15·6		
Dune slope														
Surface	0·0	0·0	26·9	—	4·4	2·1	21	0–43·9	0·1	0·1	25	0–1·0		
Subsurface	0·7	0·2	12·8	—	0·7	0·2	24	0–5·1	13·5	6·5	25	0–142·9		
Total	0·7	—	39·7	—	5·4	2·2	20	0–45·3	13·6	6·5	25	0–142·9		
Slipface														
Surface	0·4	0·2	50·9	—	91·6	53·0	25	0–1·0kg	0·0	0·0	25	0		
Subsurface	5·2	5·1	1·9	—	100·7	61·6	25	0–1·5kg	0·7	0·5	25	0–12·0		
Total	5·6	—	52·8	—	192·4	89·6	25	0–1·6kg	0·7	0·5	25	0–12·0		

M=mean; SE=standard error; n=sample number.

The data used to calculate the biomass of perennial plants is given in Appendix 1. Overall, the biomass of *S. sabulicola* and *T. hereroensis* plants per unit area was not significantly different between the 1985 and 1991 sampling periods. Individuals of each species contained approximately 1000 g.m^{-2} of vegetative material at both sampling times. However, Seely (1990) showed that the size and the density of the perennial plants varied considerably over time. The 1991 density values for both species were similar to the 1989 estimate from Seely (1990). The density of *S. sabulicola* was *c.* 11 individuals ha^{-1} and it had survived much better than *T. hereroensis* at 1 ha^{-1}. Live *S. sabulicola* plants averaged 10 m^2 in 1991 and were much larger than those sampled in the preceding years by Seely (1990). Similarly, *T. hereroensis* plants in the 1991 sample were larger than those sampled by Seely (1990) in 1978 and 1983 but similar to the average size in 1989.

The contribution of the perennial plants to the biomass of the dune slope was approximately 13 g.m^{-2}; this in combination with the quadrat biomass samples for the slope (Table 1) gave a total dune slope biomass of about 27 g.m^{-2}. Approximately 1% of the dune slope was vegetated in 1991 but biomass contained within these plants contributed half of the dune slope biomass (Table 2). The overall vegetative biomass for the dune ecosystem once adjusted for the relative area of each habitat was 13·3 g.m^{-2} in 1991. This compared with a value of 17·0 g.m^{-2} in 1985 (Table 3).

Animal biomass

Animal biomass estimated for each habitat and the four sample periods is presented in Table 4. Concentration of animal biomass shifted from the slipfaces in 1975/76 sample period to the perennial plants in the 1985/91 sample. When the relative areas of the individual habitats were taken into account, most animal biomass occurred on the dune slopes in 1985. By 1991, animal biomass on the dune had declined substantially and the interdune contained the greatest proportion per habitat (Table 5). Animal biomass was almost three times more abundant in 1985 than in 1991.

Table 2. *Contribution of perennial plants (and detritus) to biomass (g.m^{-2}) on dune slopes. Values were estimated taking into account the total vegetative biomass, plant area and plant density. The plant density and plant size values used to calculate the 1985 biomass were derived from Seely (1990)*

	Biomass (g.m^{-2})			
	1975	1976	1985	1991
S. sabulicola				
Surface plant	0·43	1·03	3·1	6·0
Subsurface plant	0·48	1·14	2·1	7·2
Total	0·91	2·17	5·2	13·2
T. hereroensis				
Surface vegetation	0·03	0·66	1·3	0·2
Subsurface vegetation	0·06	1·13	1·2	0·19
Total	0·09	1·79	2·5	0·12

There was a sevenfold increase in the omnivore/herbivores compared to the carnivores, following the good rains. This bias declined in the 1985 sample to approximately 5:1 and further in the 1991 sample to 3:1, approaching the pre-rain 1975 sample ratio of approximately 1:1.

Discussion

Both the biomass and productivity is extremely low compared to other deserts (Seely & Louw, 1980).

The hyper-aridity affects production and also slows the degradation of accumulated detritus. Effective conservation and sustainable management of this system requires that the functional processes which operate are well understood.

However, research opportunities are limited by the remoteness and fragility of the study area and the infrequency of major rainfall events. Within the central Namib Desert there has only been one major period (1976-1978) of high rain fall in the last 30 years. Consequently, a complete cycle of wet and dry years may span the lifetime of an individual researcher.

It is generally accepted that moisture controls productivity in hot arid environments (Noy-Meir, 1974; Stafford Smith & Morton, 1990) but a framework to describe the fate of biomass requires inclusion of physiographic factors and biotic consumers. Temperature, wind, soil and topography all affect evaporation and the depth to which

Table 3. *Vegetative biomass (g.m^{-2}) estimates for interdune, slope and slipface when each habitat is adjusted for the relative area occupied. The 1975 and 1976 estimates were taken form Seely and Louw (1980)*

	Vegetative biomass (g.m^{-2})			
Habitat	1975	1976	1985	1991
Interdune valley	5·1	13·8	9·3	1·3
Dune slope	0·9	19·7	5·8	11·9
Slipface	0·1	0·5	1·9	0·1
Total	6·1	34·0	17·0	13·3

moisture penetrates the soil and, therefore, the availability of moisture to the biota. Assuming moisture controls production, it is useful to divide precipitation events occurring in the Namib Desert on the basis of their effectiveness as a contributing moisture source for plants. Three types of event may be readily defined (Table 6).

Rainfall events of greater than 20 mm are necessary for the establishment of the perennial plants which only grow on the deep soft sands of the dune slopes (Seely, 1978). The large scale plant establishment which occurred during the 1976–8 wet period has not been repeated since. Heavy rain over an extended period provides moisture in the upper levels of the soil as well as allowing moisture to penetrate below the influence of evaporation. Because of the capacity for infiltration, sandy soils have a more favourable water regime for plants in arid environments compared to clay or loess soils (Noy-Meir, 1973; Kovda *et al.*, 1979;); moisture may be available to deep rooted plants of the dune slopes for several years (Noy-Meir, 1973). However,

Table 4. *Animal biomass ($g.m^{-2} \times 10^{-2}$) obtained for three habitat types during four sampling periods. The 1975 and 1976 estimates were taken from Seely and Louw (1980)*

	Annual biomass ($g.m^{-2} \times 10^{-2}$)							
	1975	1976	1985			1991		
Habitat	M	M	M	SE	n	M	SE	n
Interdune valley								
Herbivore	0·65	0·17	0·11	0·06	25	0	0	25
Omnivore	0·24	1·55	0·14	0·05	25	0·30	0·3	25
Carnivore	0·56	0·01	0·17	0·09	25	0·13	0·9	25
Sum	1·45	1·73	0·42			0·43		
Dune slope								
Herbivore	0·65	1·64	0·36	0·36	25	0	0	25
Omnivore	0·24	6·58	0·24	0·12	24	0	0	25
Carnivore	0·56	1·68	0·05	0·04	25	0	0	25
Sum	1·45	9·90	0·65			0		
Slope (including *S. sabulicola* and *T. hereroensis*)	0·8	9·9	1·68			0·26		
Slipface								
Herbivore	0·18	2·12	0·25	0·25	25	0	0	25
Omnivore	8·94	32·1	2·22	0·86	25	0·13	0·1	25
Carnivore	0·32	0·26	0·91	0·64	25	0·19	0·2	25
Sum	9·44	34·50	3·37			0·32		
S. sabulicola								
Herbivore			20·7	8·12	5	0·6	0·3	10
Omnivore			70·3	32·39	5	19·2	9·9	10
Carnivore			6·7	3·2	5	3·6	1·8	10
Sum	~0·7	~1·8	97·7			23·4		
T. hereroensis								
Herbivore			75·5	25·1	5	29·1	9·5	10
Omnivore			47·4	1·0	5	47·7	17·8	10
Carnivore			5·9	2·3	5	2·9	0·9	10
Sum	~0·5	~1·6	128·7			79·7		

M=mean; SE=standard error; n=sample number.

Table 5. *Overall animal biomass (g.m^{-2} × 10^{-2}) adjusted for habitat area plus the proportion of carnivores, herbivores and omnivores. Note that additional methods were used to obtain the animal biomass estimates for 1975 and 1976*

	Overall annual biomass (g.m^{-2} × 10^{-2})			
	1975	1976	1985	1991
Biomass in relation to habitats				
Interdune	—	—	0·23	0·24
Slope	—	—	0·74	0·11
Slipface	—	—	0·03	0·01
Total	1·25	6·33	1·0	0·36
Biomass in relation to trophic groups				
Carnivore	0·56	0·75	0·16	0·09
Omnivore	0·29	4·74	0·52	0·26
Herbivore	0·4	0·84	0·32	0·01
Total	1·25	6·33	1·0	0·36
Ratio (Omnivore + Herbivore)/Carnivore	1·23	7·44	5·39	3·0

exceptional rain events sufficient to recharge a dune aquifer may only occur in the order of once every 40 years.

Rainfall events of 10–20 mm provided enough moisture for germination and establishment of shallow rooted and quick growing ephemeral species on the slopes and interdunes (Louw & Seely, 1982; Seely, 1991). Water immediately penetrates to less than 30 cm but within a matter of days, the soil column may be wet to depths of about 1 m. Within 3 months or so, the moisture is lost from the soil. These rainfall events occur approximately every 3 to 5 years in the vicinity of the study site.

Fog and light rainfall events (< 10 mm) provide enough moisture to wet the surface of the soil for several hours (Robinson & Seely, 1980) and are probably important for the survival of invertebrates and the perennial plant species. For example, some of the invertebrates are known to fog bask or construct trenches to channel moisture (Seely & Hamilton, 1976; Seely, 1977, 1979) and the two dominant perennial plants have both surface and tap roots as well as the ability to absorb moisture through the leaves (Seely *et al.*, 1977; Nott & Savage, 1985). In addition, individual, low rainfall events (as low as ~6 mm), but not fog, may also be responsible for limited germination on the interdune or localised areas of compacted sand on the dune slopes. This amount of rain will, however, not lead to establishment or seed set and may only serve to deplete the existing seed bank.

Annual rainfall at Gobabeb is extremely low (19 mm) and variable (C.V. 113%)

Table 6. *The effect of precipitation magnitude on plant biomass production in different parts of the dune system*

	Large rainfall event (>20 mm)	Small rainfall event (10–20 mm)	Fog or light rain event (<10 mm)
Interdune	+p, +e	+e	+e*
Dune slope	+p, +e	+p*, +e	p, +e*
Slipface	–	–	–

+=germination; e=ephemeral growth; p=perennial growth; – =no plant growth; *=germination, but no establishment.

compared to deserts experiencing greater annual rainfall for example, Australian deserts (Alice Springs: annual mean 278 mm, C.V. 52%; Birdsville: annual mean 161 mm, C.V. 71%) and Israeli deserts (Negev: annual mean 87·8 mm, C.V. 109%). Fog precipitation was more predictable; however, this study has shown that substantial periods (i.e. 3 to 5 years) of fog deficit can occur and, like rainfall, may be limiting the survival of resident species if fog and rain were to be simultaneously deficient for an extended period of time.

Following the unusually heavy rain in 1976 germination of both *S. sabulicola* and *T. hereroensis* occurred over most of the formerly bare sand dunes providing approximately 4% cover. Seely (1990) recorded a decline in the survival of both species between 1978 and 1989. It is unlikely that a fog deficit contributed to the demise of *S. sabulicola* and *T. hereroensis* in the years following 1978 because fog precipitation was average or above average during the corresponding period. Decrease in soil moisture, blowout or deposition by sand (Yeaton, 1988) or natural senescence may all contribute to the decline of these species.

Given adequate moisture, plant production occurred only in the areas with largely stable substrate; little or nothing grows on the upper dune slopes and slipfaces. Seely & Louw (1980) concluded that the dune slopes were the most productive habitats after rain and the least stable, while the interdunes were the most stable habitat after rain, in terms of contribution to the total biomass of the ecosystem. However, when the individual habitats were evaluated separately the slipfaces supported the highest biomass of vegetation and animals, the vegetation being entirely in the form of detritus. In the Louw & Seely (1982) model, based upon observations made after 40 years of no major rainfall, the cycle of production, distribution and disintegration of vegetative biomass was presented relatively simply with the interdune and the slipfaces retaining biomass above 10 g.m^{-2} for around 4 decades after high rainfall events; material on the dune slope was presented as declining at almost twice the rate (Fig. 4).

In the light of the data obtained in 1985 and 1991, what alterations can be made to the Louw and Seely model? Firstly, the dune ecosystem was far more dynamic than previously envisaged. Although the biomass in the ecosystem declined at rates close to that predicted, the biomass in each of the habitats reached much lower levels than expected. Following the exceptional rain in 1978, more biomass was added to the

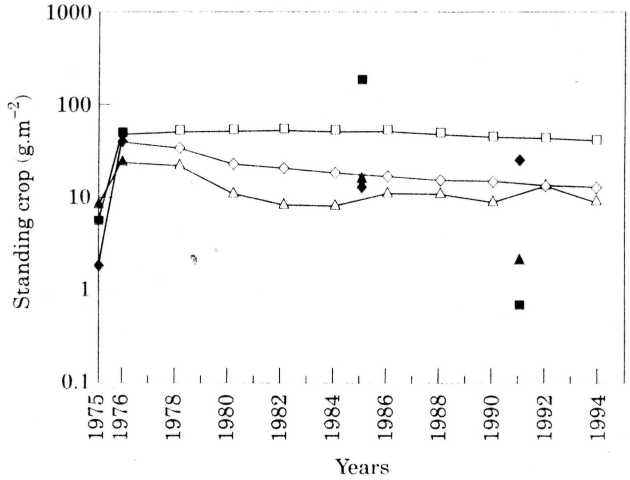

Figure 4. Changes in the standing crop (g.m^{-2}) of vegetation in the interdune (△,▲) dune slope (◇,◆) and slipface (□,■) habitats of a Namib Desert dune system following a major rainfall event. Open symbols indicate predicted change in biomass from Louw & Seely (1982) and solid symbols indicate recorded biomass values.

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system and residual above-ground vegetative biomass was abundant in the 1985 interdune and, especially, the slipface samples. However, the detritus that had existed in these two habitats in 1985 was virtually gone in 1991 and had either been consumed, trapped elsewhere or perhaps lost to photo-oxidation (Moorhead & Reynolds, 1989). In a study carried out soon after the 1976 rain event, Robinson & Seely (1980) found that detritus moved between the slipface and interdune depending on changes in wind direction and strength. It must be noted, however, that their work was carried out on small dunes where dune slope vegetation was absent.

Secondly, the dune slopes proved to be more stable than previously thought. By 1991, this habitat contained more biomass than the interdune and the slipface combined following the establishment and continued growth of perennial plants. Half was attributed to the perennial plants alone, the remainder was detritus, mostly subterranean and, of that identifiable, of perennial plant origin. It is feasible that much of the previously wind-blown detritus, of annual and perennial origin, was being trapped by the perennial vegetation and covered with sand. Under these conditions

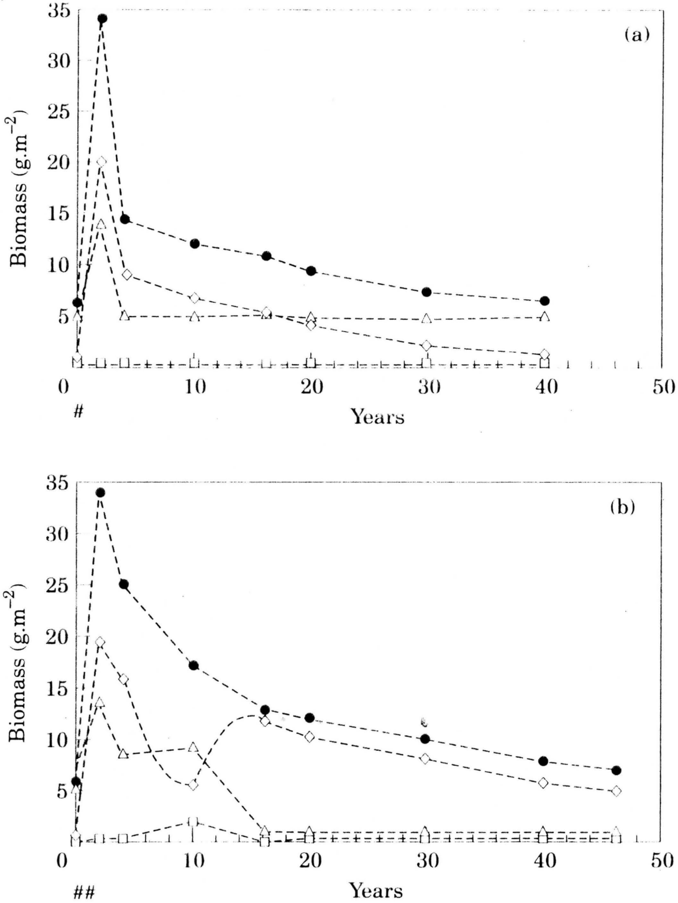

Figure 5. Vegetative biomass (g.m^{-2}) in proportion to habitat area in a Namib Desert dune system. (a) Scenario 1: few perennial plants become established on dune slopes and detritus oscillates mainly between interdune and slipface habitats. (b) Scenario 2: many perennial plants become established on the dune slopes. Continued growth of these plants contributes a substantial amount of biomass to the dune system and their large size traps biomass which would otherwise move between the interdune and slipface habitats. (△) = interdune; (◇) = slope; (□) = slipface; (●) = total; # indicates > 20 mm of rain in a 5-day period.

material would be released slowly into the system with the death and decay of *S. sabulicola* and *T. hereroensis* and movement of the dune surface.

By contrasting these observation with those of Seely & Louw (1980), it is evident that the pattern of biomass retention and distribution in the central Namib Desert may follow one of two scenarios depending on the ability of perennial plants to become established (Fig. 5). If perennial plants fail to become established after rain, the plant material produced on the interdune or dune slopes, once in detritus form, would oscillate between the slipface and interdune habitats until it has been consumed by the resident detritivores (Scenario 1). If, alternatively, perennial plants become established and continue to grow on the dune slopes, their presence would effectively create a net to catch material moving between slipface and interdune. The biomass produced by the perennial plants is also added; *S. sabulicola* material would probably be of lower nutrient value and less easily consumed than ephemeral plant matter; decomposition and reversion to the state described in the previous scenario would possibly take up to four decades (based on one record period only) if dry conditions persisted (Scenario 2).

Additional census methods used in the 1975/76 may explain larger biomass values compared to the 1985 and 1991 samples. As indicated by the 1975/76 data, however, this is unlikely to affect the general trends and ratio of trophic groups.

The distribution and abundance of animal biomass generally reflected the distribution of plant biomass with the exception of animal biomass on the interdune. Biomass in this habitat remained high and comparable to the 1985 estimate; greater nutrient concentration and substrate stability may provide an explanation. The germination and establishment of annual vegetation with low rainfall, as occurred three times between the 1985 and 1991 measurements, may also help explain the values obtained. A decline in overall animal biomass between the 1985 and 1991 samples corresponded with the reduction of plant biomass over the same period. This change was mirrored in the ratio of carnivores to herbivores and omnivores; it could be expected that the value would approach parity with the decreasing availability of plant biomass.

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Appendix 1. *Vegetative biomass, density and plant size for* S. sabulicola *and* T. hereroensis

Table A. *Vegetative biomass (g.m*$^{-2}$*) obtained for* S. Sabulicola *and* T. hereroensis *from three sample periods*

	Vegetative biomass (g.m^{-2})								
	1976			1985			1991		
	M	SE	n	M	SE	n	M	SE	n
S. sabulicola									
Surface	354·2	60	5	522·5	159·3	5	495·0	111·2	10
Subsurface	394·4	184	5	342·5	98·8	5	594·3	95·9	10
Total	748·6	—	5	865·9	254·6	5	1089·3	136·9	10
T. hereroensis									
Surface	408·2	72	5	466·9	81·2	5	530·7	53·1	10
Subsurface	699·3	160	5	455·7	80·7	5	531·8	109·3	10
Total	1107·5	—	5	922·6	80·3	5	1062·5	147·8	10

Table B. *Estimates of the density and area of perennial plants in 1985 and 1991. The 1985 estimates were derived from Seely (1990). For 1991, the density estimates were derived from six transects (each 1000 m x 190 m) and the plant area was estimated from length and breadth measurement of individuals. The size of dead* T. hereroensis *plants was not measured because only a relatively small amount of biomass remained*

	Density (plants. ha^{-1})				Plant area (m^2)			
	1985	1991			1985	1991		
	M	M	SE	n	M	M	SE	n
S. sabulicola								
Alive	14	11·2	3·1	6		9·9	2·31	40
Dead	10	7·8	1·7	6		2·66	0·47	40
Total	24	19·3	2·6	6	2·5	6·28	1·24	80
T. hereroensis								
Alive	3	0·3	0·1	6				
Dead	8	0·8	0·4	6				
Total	11	1·1	0·5	6	2·5	3·2	0·71	40

M=mean; SE=standard error; n=sample number.