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rnal of Arid Environments (1980) 3, 25–54

First approximation of the effects of rainfall on the ecology and energetics of a Namib Desert dune ecosystem

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Accepted 1 October 1979

Ecological surveys, conducted after a prolonged dry period (mean annual precipitation—14 mm) and after a high rainfall event (118 mm), showed that the Namib dunes respond dramatically to rain. Prior to rain the biomass of plants measured 2·6 g m^{-2}, of detritus 0·4 g m^{-2} and of animals 0·01 g m^{-2}. These figures represent the lowest biomass data reported for any terrestrial ecosystem. After rain the potential energy contained in the plant biomass increased ninefold while the potential energy in the detritus and the animal biomass increased sevenfold and sixfold, respectively. This sudden increase in biomass was largely due to the rapid growth of ephemeral grasses. Rain decreased the extreme patchiness of the biota by causing niche overlap, expansion of the home ranges of animals and a change in distribution patterns of plants.

The various habitats within the dune ecosystem differ markedly with respect to both productivity and stability. The dune slope is the most productive and the least stable, while the interdune valley is the most stable and the second most productive, in terms of contribution to the total biomass of the ecosystem. However, when the individual habitats are evaluated separately, the slipface supports the highest biomass of vegetation and animals, the former being entirely in the form of detritus.

The most important limiting factors identified were water, and the nitrogen and phosphorus content of the dune sand as well as the physical stability of the sandy substrate in certain habitats. The wide trophic ratios established between animal biomass and the biomass of plants and detritus (1 : 249) suggest that available energy does not limit the size of herbivore and omnivore populations. In contrast, the low protein content of the vegetation during dry periods (3·1 per cent) is considered to be an important limiting factor. During both dry and wet periods, available energy may, however, limit carnivore populations.

Unique features of the ecosystem are to be found in the absence of a significant microbiological decomposition loop, the degradation of large amounts of accumulated detritus by tenebrionid beetles, the dependence of the biota on fog and the physiological and behavioural characteristics of the fauna. These include fog imbibition, fog basking and water storage which enhances their opportunism in exploiting the erratic resources of this unusual ecosystem.

Introduction

Although a considerable amount of knowledge has been documented with respect to the taxonomy and the physiological ecology of the Namib biota, no attempt has as yet been made to describe the general ecology of this region quantitatively. Moreover, to the best of our knowledge, a quantitative analysis of the ecology of a desert dune system has not been undertaken to date and the purpose of this paper is to fill this gap.

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0140–1963/80/010025+38 $02.00/0
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The Namib Desert extends some 2000 km along the south western coast of Africa from approximately the Olifants River in the Cape Province to Moçammedes in Angola (Goudie, 1972) and is the only true desert in southern Africa. It is situated within the south western arid zone which covers half of southern Africa and the aridity of this coastal desert is further intensified by the presence of the cold Benguela current on the west coast. Rain is therefore a very infrequent occurrence while fog occurs more regularly.

Within the large dune system in the southern part of this desert, an exceptional fauna has evolved despite the limited resource base. For example, the vegetationless portions of the dunes are inhabited inter alia by several species of tenebrionid beetles and a lizard which feed on wind-blown plant detritus and exhibit unusual, if not unique, behavioural adaptations that allow them to utilize the fog as a moisture source (Koch, 1961, 1962; Louw, 1972; Seely, 1978*a*, 1979). This apparently unique life-style has not been described in any other dune system of the world. Several other related species occupy the lightly vegetated lower portions of the dunes and the interdune valleys. These species include mostly tenebrionid beetles, arachnids and reptiles (Lawrence, 1959). Earlier descriptive studies of this system have been published by Koch (1961, 1962), Kühnelt (1965) and Holm (1970). The purpose of this study was to evaluate in quantitative terms the effect of rainfall upon the ecology of this dune ecosystem. A preliminary bio-energetic analysis has been presented for a very dry period as well as for a period following unusually heavy rainfall. We have concentrated on those species resident in the dune ecosystem but regular visitors have also been included in the discussion. Because of the considerable diversity and extreme patchiness in the distribution of the biota within the dune ecosystem as a whole, this paper applies in detail only to the area which was investigated.

The study area and biota

Abiotic environment

Although the Namib extends over 2000 km along the Atlantic coast, sand dunes cover less than half of the total area. The dune sea is composed mostly of linear dunes running predominantly in a N–S direction (Plate 1). From west to east the linear dunes become more widely spaced and the surface of the interdune valleys (dune streets) changes from sand to a sandstone and calcrete rubble surface.

The study area was selected within the southern dune system in the vicinity of Gobabeb (23°34′S, 15°03′E) on the northern margin of the dune mass, 60 km from the coast (Fig. 1). The dune study site therefore borders on two other desert habitats within the central Namib, namely the riverine habitat supported by underground water beneath the dry Kuiseb River bed, and the flat gravel plains to the north of that river. The clear demarcation between the dunes and the latter two habitats can be seen in the satellite photograph (Plate 1). Although the abiotic features of the dune system in this area have been recently described in detail by Robinson & Seely (1980), a brief description of these features is pertinent to this discussion.

The dune system can be divided into various habitats based both on the physical morphology of the dunes and the distribution of the biota. The following broad classification has frequently been employed: the interdune valleys, the vegetated lower portion of the dunes consisting of the dune base and plinth, and the vegetationless dune crest system (Plate 2). In the study area the interdune valleys between the linear dunes are stoney and are only occasionally covered by sand. The average distance between dunes is 1·8 km and the average height 80–100 m (Goudie, 1972). The linear dunes in this area have a relatively stable base with only the upper portion being mobile. As the prevailing wind direction varies with the season, the shape and location of the slipfaces and crests adjust accordingly.

The climate varies over the southern dune sea from a predominantly winter rainfall regime in the south to a summer rainfall regime in the north where the study was undertaken. Precipitation from fog is greatest near the coast decreasing further inland, while precipitation from rainfall shows the opposite pattern and decreases markedly from east to west. At the study site the combined precipitation from fog and rain is at a minimum in view of its central location on an east-west transect across the desert. Here thec limate is characterized by frequent but irregular morning fogs and high diurnal ranges of temperature and humidity. Average cloud cover is 41 per cent at 0800 h and 18 per cent at 1400 h SAST time; thus direct radiation is high throughout most of the day (Schulze, 1969). Wind is an important abiotic factor in Namib dune ecology. Not only do the winds sculpt the dunes, thereby shaping habitats, but they also transport detritus in the form of dried grass into the dunes and either cool or heat the environment, depending on the wind direction.

In view of the important effects of insolation and wind upon the surface of the dunes, the micro-climate near the surface differs dramatically from standard meteorological data. An illustration of this difference is provided by a typical temperature profile recorded for a dune within the study site (Fig. 2).

Biotic environment

The composition of the biotic environment is often dependent on the characteristics of the sandy substrate. Those species of animals resident in the sand-dune habitat do not occur either in the riverine sand or the gravel plains, although they are in close proximity to one another. Several grass species may, however, inhabit both the dune and riverine sand habitats. There is also a slight overlap between the inhabitants, both plant and animals, of the harder-surfaced interdune valleys and the gravel plains to the north of the river. In addition to the substrate-dependent, resident species in the dunes, there are a number of larger mobile animals that enter the dune system occasionally.

Vegetation

The vegetation of the dunes and interdune valleys of the northern end of the major dune sea, including the study area, has been briefly referred to by Giess (1962, 1971) and more recently the phytosociology of the area has been described by Robinson (1976). In the latter study Robinson differentiates four communities, namely the *Stipagrostis sabulicola* community, the *S. gonatostachys* community, the *S. lutescens* community and the *Acanthosicyos horrida* community, the first three species being grasses and the fourth a cucurbit. Robinson's study was, however, carried out during a dry period and therefore only the stable elements of the dune community were included, with the exception of *S. gonatostachys* which germinates after very little rain. Two of these four communities were included in the present study.

Sufficient rain for germination appears to be the limiting factor for the presence of most vegetation in the dunes (Seely, 1978*b*). Fog, however, is important for the survival and continued growth of the succulent *Trianthema hereroensis* (Seely *et al.*, 1977) and the coarse grass *S. sabulicola*. In the study area, some 60 km inland, the latter two plants are the only dune species which survive during normal prolonged dry periods. Other elements of the flora are ephemeral, surviving for a number of years following an above average rainfall but disappearing from the dune habitat during a prolonged dry period.

Fauna

The fauna of the dune system is typically desertic and is composed almost entirely of insects, arachnids and reptiles. Although certain important morphological adaptations are exhibited by some of these animals, particularly to locomotion and life in a sandy medium, the most important adaptations for survival within the dune system are of a behavioural and to some extent a physiological nature. In view of the key importance of these attributes to survival within the system further discussion is warranted.

Adaptation to tolerance of high temperatures is only found in the oryx or gemsbok *Oryx gazella*, a large antelope that enters the dune system for long periods when food is abundant. All other diurnal species in the dunes either evade direct solar radiation by using the very sparse vegetation as shade (e.g. Cape hare, *Lepus capensis*) or escape the unfavourable temperatures completely by retreating beneath the surface of the sand, where conditions of temperature and humidity remain tolerable throughout the day. The latter behaviour is used by the majority of the resident dune species (Koch, 1961; Louw & Holm, 1972), although some species will use both behaviour patterns when conditions are less extreme (Henwood, 1975).

Adaptations to minimize water loss have not been studied extensively in Namib dune species. Nevertheless, Edney (1971) has shown that certain species of Namib tenebrionids exhibit some of the lowest transpiration rates recorded for any arthropod. Moreover, by retreating below the sand surface where humidity is higher, water loss is further reduced (Holm & Edney, 1973).

Adaptations to facilitate water uptake by Namib dune animals have long been a matter of speculation (Koch, 1961; Lawrence, 1965). More recently it has been shown that the side-winding adder *Bitis peringueyi* drinks fog droplets which have precipitated on the dorsal surface of its own body (Louw, 1972; Robinson & Hughes, 1978). The sand-diving lizard, *Aporosaura anchietae*, drinks fog droplets clinging to the sparse dune vegetation and stores this water in its body for long periods (Louw, 1972; Robinson, 1979). The silverfish *Ctenolepisma terebrans* is able to absorb water vapour from air at 47·5 per cent r.h. and above (Edney, 1971). The relative humidity of the air between the sand grains reaches this level frequently (Holm & Edney, 1973). The tenebrionid beetles of many species make use of irregular advective fog and occasional dew moisture which they obtain from droplets condensing on stones or vegetation, from moist sand or by fog basking (Hamilton & Seely, 1976; Seely & Hamilton, 1976; Seely, 1979).

Spatial and temporal adaptations to an unstable or patchy environment are, as expected, also exhibited by the Namib fauna (Holm & Edney, 1973). Some species only metamorphose and become active on the surface in an adult form after sufficient rain has fallen (Holm, 1970), an event which does not occur every year. Most of the dune species are present throughout the year but clearly increase their numbers during high rainfall years. Also, those species which have been studied to date, *A. anchietae* and the tenebrionid beetle *Onymacris plana*, show increased deposition of fat during high rainfall seasons (Robinson, 1979; personal observation).

Generally, the Namib fauna, employing various adaptations, evades the extreme climatic conditions of the dune desert while exploiting irregular pulses of food and water. Certain large animals tolerate the climatic extremes while others, mainly invertebrates, avoid unsuitable conditions, which may include lack of food, by being ephemeral. Opportunism, when food is abundant, combined with energy-saving adaptations during periods of nutritional stress are therefore key adaptations for the survival of the fauna.

Procedure

This investigation was initiated fortuitously at the end of a prolonged dry period in 1975 (average rainfall 14 mm, range 2·2–30·3 mm, over 13 years; Meteorological records, DERU). During January to March 1976, 118 mm of rain fell at Gobabeb resulting in germination and an unprecedented growth of vegetation. This represented the highest recorded precipitation in the central Namib since 1934. The sudden increase in the amount of vegetation was followed by an equally dramatic increase in the size of some of the animal populations. Therefore, by carrying out surveys both before and after the heavy rainfall event, the effect of rainfall could be evaluated on the basis of the increase in the biomass of both plants and animals.

The study site was selected because of its location in the driest portion of the central Namib and because of its proximity to the research station at Gobabeb, where considerable research has been focused. For the purpose of this study the dune ecosystem was broken down into three main habitats: the interdune valleys, the slipfaces and the dune slopes (Plate 2). Two sub-habitats of the dune slopes, namely the *Stipagrostis sabulicola* and

Trianthema hereroensis sub-habitats (Plate 3), were also differentiated. This division was based upon the distribution of detritus, plants and animals and combines the dune base and plinth described by Robinson & Seely (1980) within the dune slope habitat.

In this paper we refer to standing plants, whether dead or alive, as plants, to wind-blown plant material as detritus and to the combination of both plants and wind-blown detritus as vegetation. The term omnivore has been applied to those animals, predominantly tenebrionid beetles, but also lizards and birds, that consume plants, detritus and animal material. In some instances the term detritivore may have been more appropriate as, for example, in the case of certain tenebrionids which exist mainly on detritus during prolonged dry periods. The term carnivore has been applied to any animal feeding on live animal prey exclusively. The use of the term herbivore has been restricted to those animals which predominantly consume plant material and therefore excludes most animals feeding predominantly on the wind-blown detritus because many of the latter group will also consume animal carrion when the rare opportunity arises to do so.

Classification of dune habitats

The interdune valleys

These are relatively level areas, sometimes referred to as dune streets, with a lightly consolidated sandstone and gravel substrate (Plate 2). The predominant vegetation cover is composed of *Stipagrostis ciliata* and *S. gonatostachys*, both ephemeral grasses which can behave as perennials if growing in a very favourable locality. The animal species occurring in the interdune valley are more ephemeral than those in the other habitats.

The dune slope

This habitat includes the sandy substrates of the dune base and plinth of the leeward slopes, the windward slopes and the mixed transverse dunes of the predominantly linear dune habitat (Fig. 1). Here the sparse vegetation during dry (normal) periods consists of the dune grass *Stipagrostis sabulicola* and the leaf succulent *Trianthema hereroensis*. During wet periods two quasi-ephemeral grasses, *Asthenatherum glaucum* and *Eragrostis spinosa*, germinate and persist for several years before dying off in the absence of further rains. *S. gonatostachys* occurs on the lower slopes also, but to a lesser extent than in the interdune valleys. The geophyte *Monsonia ignorata* occurs predominantly on the lower leeward slopes. Another vegetative component, wind-blown plant detritus, is a very important part of the resource base during both dry and wet periods.

The slipface

The slipfaces are a focal point for animal activity and were consequently selected as the third main habitat to study. Wind-blown detritus tends to collect preferentially on the slipfaces. Because of the steep angle (32°) of the slipface, turbulence is created in the laminar flow of air and both detritus and sand fall out of the air stream into the relatively calm wind-shadow of the slipface (Bagnold, 1954; Robinson & Seely, 1980). Also, the sand on the slipface has not been compacted by wind, as is the case on the dune slopes; it is loosely packed, well aerated and therefore an ideal medium for burrowing and sand diving.

The Trianthema hereroensis *and* Stipagrostis sabulicola *sub-habitats*

Because these perennial plants provide very important, although widely scattered, focal points for life in the dune ecosystem, they were included in this study as sub-habitats of the dune slope and sampled systematically.

The large perennial cucurbit *Acanthosicyos horrida* or Nara is also an important focal point for animal life in the dunes. For example, one plant which occupied an area of 230 m^2, harboured over 2200 individuals of the beetle *Onymacris plana*. In view, however, of its very marginal distribution in the dune ecosystem as a whole, *A. horrida* was not included in the study site or survey.

Using planimetry and aerial photography the respective surface areas occupied by the different dune habitats were measured. These values were then used to calculate the contribution of the biomass from each habitat to the ecosystem as a whole.

Sampling techniques

In view of the extreme patchiness in the distribution of both plants and animals, we realised at the beginning of the investigation that neither a single sampling procedure nor standard sampling techniques would suffice. For this reason, several techniques were employed both for comparative purposes and also to supplement one another. When data are reported the relevant sampling procedures have been designated.

(1) *Excavation*

This technique was selected mainly to provide an estimate of the detritus component of the resource base, which is a particularly important component during a dry period and also to provide an estimate of the below-ground biota. For each of the three main habitats, five or six excavations were made at randomly selected localities. At each excavation locality, on the windward slope and interdune valley, a 20 × 20 m square was measured out and approximately one square meter was excavated to a depth of 20 cm at each corner and in the centre of each of these squares, thus providing a total of 25 excavations per habitat. On the slipfaces the selection of the site was dictated by the geometric characteristics of the slipface. Two excavations were made at the base, two at the crest and one in the middle of the slipface. The total area of the slipface was then measured and this figure used to calculate the average biomass on each slipface. Boards, held in place by iron rods, were used to prevent sand filling in the excavation while the excavation was in progress. The exact dimensions of the area encompassed by the boards were measured at the completion of the procedure. All excavated sand was passed through a sieve of 1·0 mm mesh. The sand which passed through the sieve was then mixed and a sub-sample (20 litres) was then passed through a sieve of 0·7 mm mesh. All plant and animal material was removed from the sieve, the animals were preserved in alcohol for later drying, weighing and analysis. The plants were stored in paper bags for later treatment.

At an early stage of the investigation it became clear that in view of the very patchy distribution of the slipface fauna, particularly the lizard *Aporosaura anchietae*, that the excavation technique in the slipface habitat would have to be supplemented. The estimate of animal biomass was therefore supplemented by locating seven observers equidistantly along the upper perimeter of the slipface and allowing them to move down the slipface while they excavated the sand systematically for a timed period of five minutes. These data were also supplemented by data from a study on the population dynamics of *A. anchietae* (Robinson, pers. comm.).

(2) *Plant excavation*

Five randomly selected individuals of both *S. sabulicola* and *T. hereroensis* were excavated. Prior to excavation, a plastic sheet was used to enclose the plant completely and pyrethrum insecticide sprayed into the enclosed area. All arthropods were collected from the sand surface. Boards, supported by rods, were placed in the sand around each plant and excavated to a 20 cm depth as previously described. The entire plant including the roots was removed and placed in a plastic bag. The plant material was returned to the laboratory and all arthropods carefully removed. The plants and animals collected from the excavations were identified as closely as possible and dry weights and energy values were determined. In addition, the total number of plants of the two species were counted along a 5·5 km stretch of windward slope (average distance to top of dune—190 m). These data were then combined with the excavation data to calculate the biomass for the sub-habitats and ecosystem as a whole.

(3) *Transect census*

A second method of estimating the biomass was employed within the same habitats to supplement the excavation technique. All animals were counted along a transect of 500 × 15 m in the interdune valley and an area of 15 × 15 m was intensively searched by turning over pebbles and stones. This was carried out at hourly intervals for 11–15 h by three observers progressing along a straight line. If any animal species encountered in this survey had not been collected during the excavations, 20 individuals were collected for dry weight and energy determinations and final inclusion in the biomass estimates.

A similar procedure was employed on the windward slope with the exclusion of the intensive search, as there were no surface pebbles to serve as shelter for animals.

In the slipface habitat a different procedure was employed From the crest of one typical slipface the animals of each species were counted every 10 min in a measured area which could be easily scanned with 10 × 40 binoculars without disturbance to the animals.

The data obtained from the transect census technique incorporated an inherent error as some animals are always below the surface at any one time. To minimize this error, the maximum number of any species observed in one hour was used for that species to calculate biomass.

Some consideration should be given to the possible rôle of the oryx in the utilization of the plant biomass. Although ungulates of this size are capable of removing large amounts of herbage in a short period of time, the biomass of oryx in the dunes is very low and we were unable to obtain reliable census figures. Rough estimates based on preliminary census figures and using suitable regression equations suggested that relatively small amounts of the total standing crop could be removed by these animals. In consequence their rôle in the ecosystem has been excluded for the purposes of this study.

(4) *Clipping of vegetation*

Although the methods used during the dry period were repeated during the wet period, no provision had been made during the dry period for assessing ephemeral grasses which had been totally absent then. Therefore during the wet period plots were clipped to surface level on the interdune valleys and dune slopes. Because of the uniformity of the interdune valley grass cover, as reflected in the standard deviation, eight plots 25 × 25 cm were clipped. On the dune slopes, where the vegetation was extremely patchy, 20 localities were clipped. At each locality a plot measuring 5 × 5 m was clipped on the lower third of the slope where the vegetation was most dense and uniform, a plot 5 × 10 m on the middle third and a plot 5 × 15 m on the upper third where the vegetation was most patchy. In this way 0·16 per cent of the area over 9 km of dune slope was sampled. Two localities were selected per kilometer using a table of random numbers and the location of the NW corner of each plot was selected in the same way. The plants clipped were separated to species in the field and wind-blown detritus was collected from the sand surface. Dry weights were then determined.

(5) *Distribution of plants within the dune slope habitat*

Two dunes of slightly differing configuration were selected within the study area for vegetation profiles. A traverse was made of each dune and the percentage cover of each plant species was estimated for a 5 m wide transect broken down into 10 m intervals. The angle of slope was measured along the same traverse at 5 m intervals using an M.C. Clinometer (Hilger & Watts Ltd., England).

(6) *Calculation of biomass*

All plant and animal material from the excavations, census surveys and clippings was dried and weighed and dry weight per unit area of habitat was determined. Using these values and the percentage surface area occupied by the various habitats within the ecosystem, the biomass per unit ecosystem was calculated.

(7) *Energy values*

Animals preserved in alcohol or formalin and plant material were dried and energy values were determined in an adiabatic bomb calorimeter or microbomb. Average values were used for arthropods in the few instances where the sample size was too small for accurate calorimetry.

(8) *Food webs*

These have been constructed using personal observations, literature references (Holm, 1970; Kühnelt, 1965; Louw & Holm, 1972; Robinson, 1978), stomach analyses and scat analyses. Only major pathways of energy transfer have been indicated because of the large degree of opportunism which exists within the dune faunal web.

(9) *Meteorological observations*

The study site is located within 10 km of a First Order Weather station at Gobabeb. Data from these instruments as well as from the Lambrecht recording rain gauge and the Fuess–Robitz radiation recorder were used in this study.

(10) *Statistics*

Means, standard errors of the mean and standard deviations were calculated for all average figures. The significance of differences between variances was calculated using a two-tailed *F*-test. Because the *F*-test often indicated that the variances were significantly different a modified *t*-test, taking this into consideration, was used to test the equality of the means of two samples (Sokal & Rohlf, 1969: pp. 374–5).

Results

Relative areas occupied by the three main habitats

The three main habitats (Fig. 1 and Plate 2) occupied markedly different proportions of the dune ecosystem. The interdune valley comprises 55 per cent of the ecosystem and therefore represents the largest habitat in the study area. The dune slopes represent 44 per cent when the windward slopes (14 per cent), the leeward slopes (12 per cent) and the irregular dunes (18 per cent) are combined. The smallest area is occupied by the slipfaces which constitute only 0·97 per cent of the dune ecosystem. The degree of patchiness in the distribution of the biota varies between habitats and therefore the differing proportions of the ecosystem, occupied by the various habitats, has an important effect on the overall patchiness of the ecosystem.

Effect of rainfall on biomass and distribution of plants and detritus

Figure 3 compares the biomass of plants and accumulated detritus, above and below the sand surface, in the various habitats during a dry (normal) period and after rain. Energy values have also been included. These results show that the total vegetation (plants and detritus) increased 9·4 fold on the slipface, 53·0 fold on the dune slope and 2·7 fold in the interdune valley. Also, estimates derived from total counts combined with excavations of the individual plants, indicated that the *S. sabulicola* biomass increased 2.4 fold and that of *T. hereroensis* 19-fold.

When the biomass of plants and detritus within each habitat is adjusted for the relative area occupied by each habitat, the contribution of each habitat to the ecosystem as a whole can be calculated (Fig. 4). These results show that, in spite of being the richest habitat when the habitats are judged separately, the contribution of the slipfaces to the ecosystem as a whole is now the lowest. In contrast, the contribution of the interdune valley now becomes the greatest followed closely by the dune slope. These results are naturally related to the relative areas occupied by the various habitats within the ecosystem. In the case of the sub-habitats (*T. hereroensis* and *S. sabulicola*), no marked change occurs when making the above

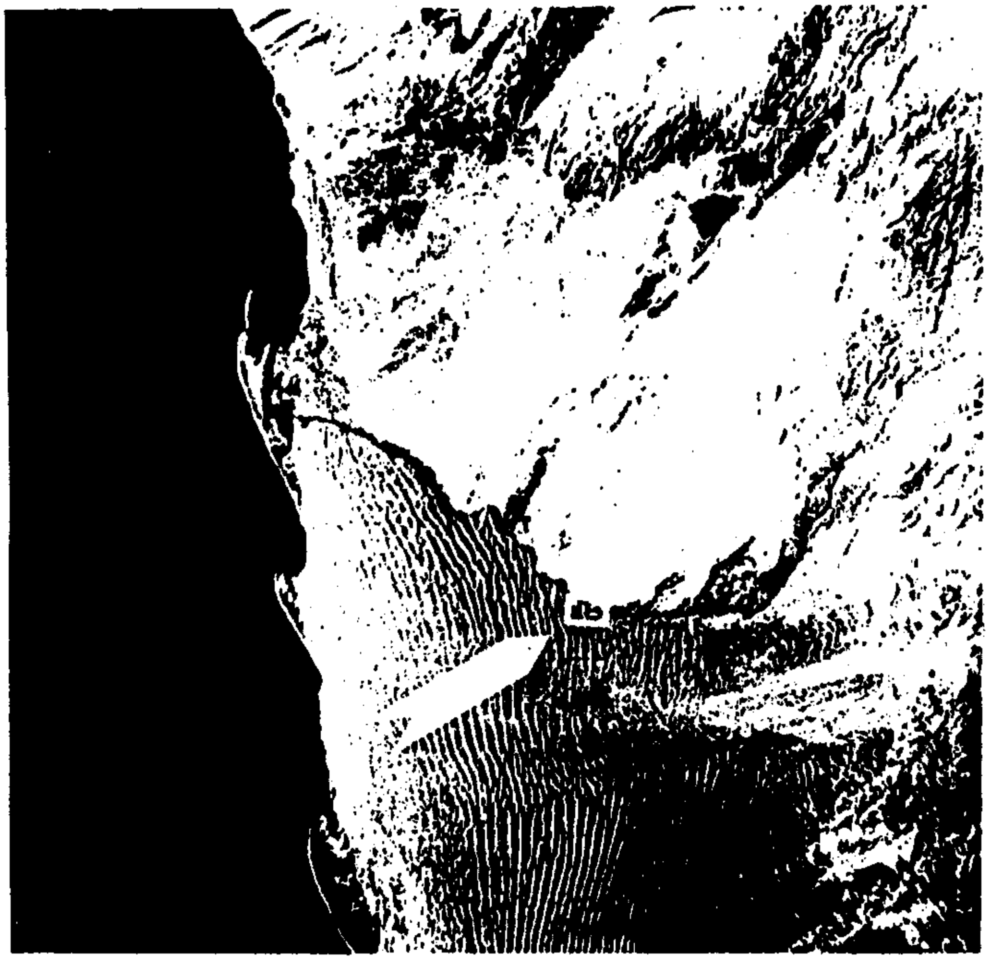
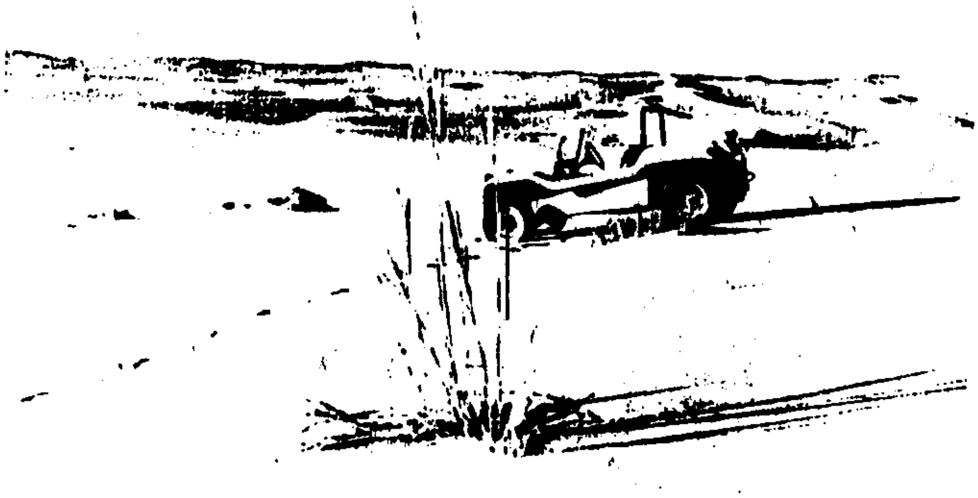


Plate 1. Satellite photograph of central Namib Desert showing sharp demarcation between dune, riverine and plains habitats, and location of study site.

(a)



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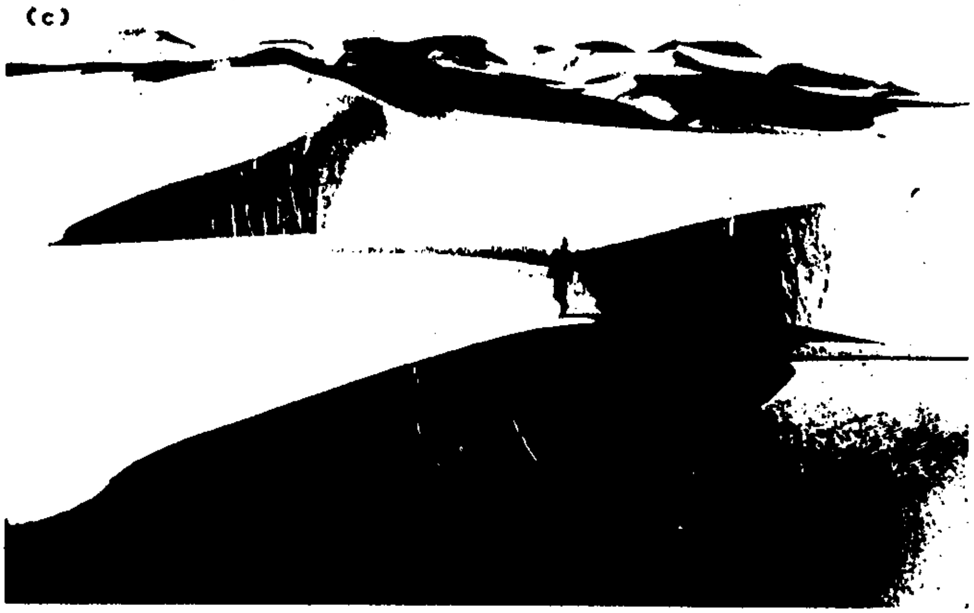

Plate 2. The three main habitats within the study site: (a) dune slope during dry period; (b) interdune valley after rain and (c) slipface.

(a)

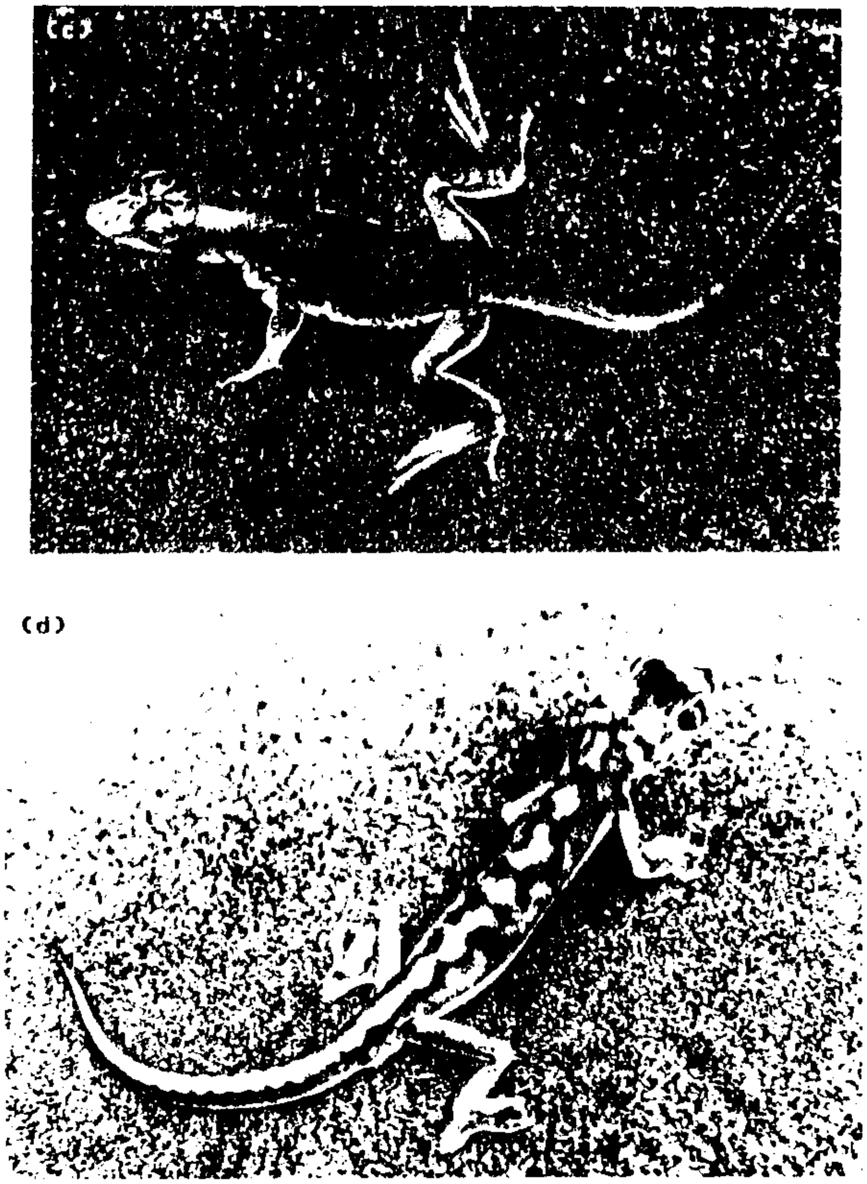

Plate 5. Representatives of the endemic ultrapsammophilous fauna of the Namib dunes which exhibit a marked degree of opportunism and flexibility in exploiting this unusual environment. (a) Fog-basking tenebrionid beetle *Onymacris unguicularis*; (b) the disc-shaped tenebrionid *Lepidochora discoidalis* building a sand trench for later extraction of fog water; (c) the sand-diving lizard *Aporosaura anchietae* which stores large amounts of fog water in its body; (d) the gecko (*Palmatogecko rangei*) with webbed feet to facilitate locomation and digging in the sand dunes.

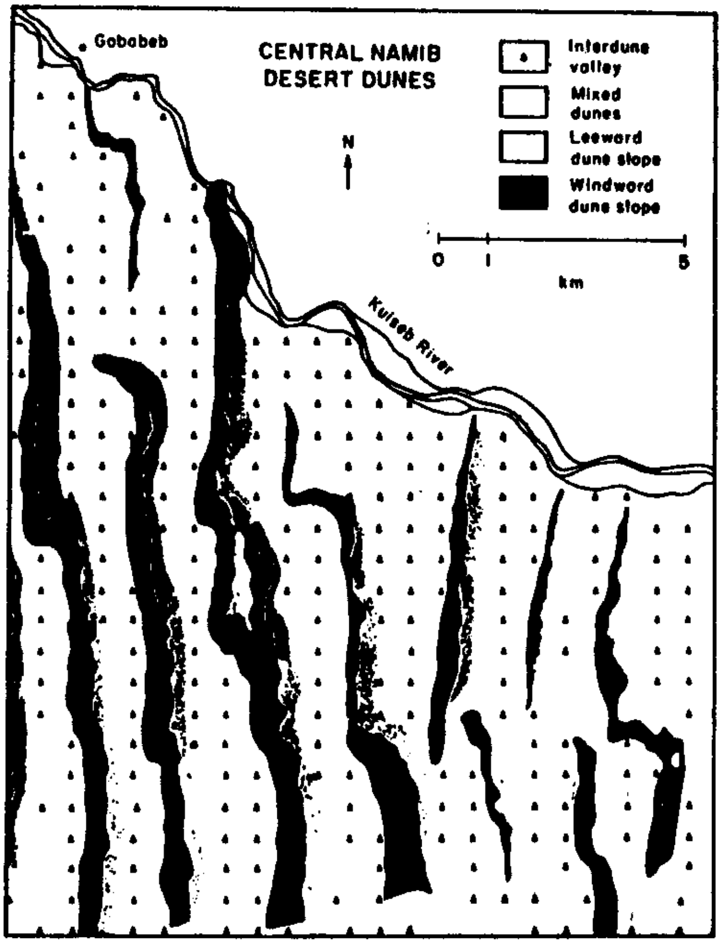

Figure 1. Topographical map of study site showing linear dunes and distribution of habitats.

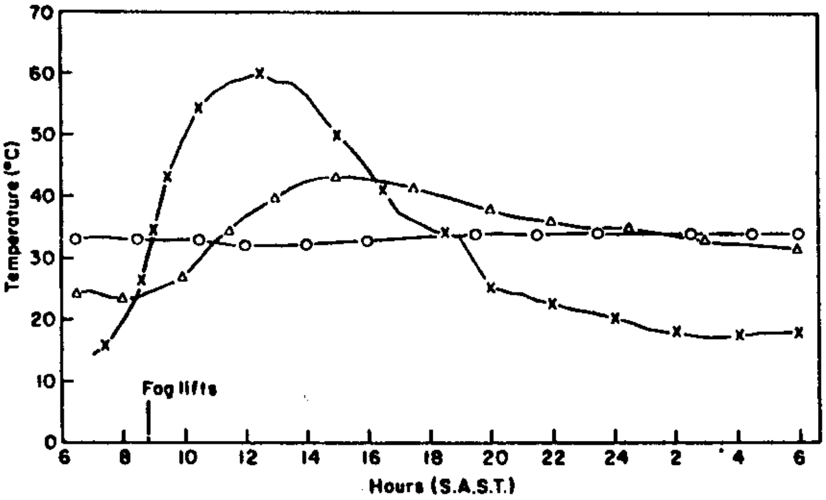

Figure 2. Temperature profile of a dune during and after the occurrence of advective fog. ×, Surface temperature of slipface facing ENE; △, temperature at 10 cm below surface; ○, temperature at 20 cm below surface (Summer, 16–17 December 1977).

adjustments. In absolute terms an individual *S. sabulicola* represents an average concentration of plant material and detritus of 354·2 g m^{-2} (s.e. ± 60) above surface and 394·4 g m^{-2} (s.e. ± 184) below surface. An individual *T. hereroensis* represents an average concentration of plant material and detritus of 408·2 g m^{-2} (s.e. ± 72) above surface and 699·3 g m^{-2} (s.e. ± 160) below surface.

Table 1. *Statistical analysis of increase in biomass from dry to wet period of plants and detritus. Data were obtained by the excavation method and transect counts*

Habitat	Biomass (g m^{-2}) (dry year) $\bar{x}$	±s.e.	N	Biomass (g m^{-2}) (wet year) $\bar{x}$	±s.e.	N	Statistical significance (P) F	t
Interdune valley								
Surface vegetation	4·4364	1·4500	25	23·1725	3·0374	25	0·001	0·001
Subsurface vegetation	4·9469	1·1600	25	1·9734	0·3203	25	0·001	0·02
Surface detritus	0	—	25	0	—	25	—	—
Subsurface detritus	0	—	25	0	—	25	—	—
Σ	9·3833			25·1459				
Dune slope								
Surface vegetation	0	—	30	23·2695	8·6541	25	—	0·02
Subsurface vegetation	0	—	30	11·4191	4·0593	25	—	0·01
Surface detritus	0	—	30	3·6899	1·9776	25	—	NS
Subsurface detritus	0·7092	0·2021	30	1·3604	0·8169	25	0·001	NS
Σ	0·7092			39·7389				
Slipface								
Surface vegetation	0	—	25	7·0016	35·0081	25	—	NS
Subsurface vegetation	0	—	25	1·8278	1·7684	25	—	NS
Surface detritus	0·4051	0·2017	5	43·8817	28·9603	25	0·001	NS
Subsurface detritus	5·2283	5·0994	25	0·1078	0·0792	25	0·001	NS
Σ	5·6334			52·8189				
S. sabulicola								
Surface vegetation	0·4326	0·0724	5	1·0221	0·1711	5	NS	0·02
Subsurface vegetation	0·4833	0·2265	5	1·1418	0·5351	5	NS	0·02
Surface detritus	0·0023	0·0002	5	0·0054	0·0040	5	NS	0·02
Subsurface detritus	0·0009	0·0004	5	0·0021	0·0009	5	NS	0·02
Σ	0·9191			2·1714				
T. hereroensis								
Surface vegetation	0·0327	0·0059	5	0·6180	0·1107	5	0·001	0·001
Subsurface vegetation	0·0581	0·0012	5	1·0980	0·2443	5	0·001	0·001
Surface detritus	0·0022	0·0008	5	0·0416	0·0152	5	0·001	0·001
Subsurface detritus	0·0016	0·0009	5	0·0302	0·0178	5	0·001	0·001
Σ	0·0946			1·7878				

In addition to the biomass figures reported above, the distribution of the plants and detritus also warrants comment. The dune slopes are the least homogeneous in this respect. *S. sabulicola* and *T. hereroensis* cover less than 1 per cent of the dune slope surface area, yet they constitute 59 per cent of the biomass of plants and detritus during the dry period and only 9 per cent during the wet period. The distribution of detritus on the slipface was far less influenced by rain. For example, using the excavation method, more than 99 per cent of the total detritus was found at the base of the slipface during both the wet and the dry period, although this area constitutes only 10 per cent of the total slipface. It was only in the interdune valley that any semblance of uniformity in the distribution of the vegetation was found. All these results serve to illustrate the extreme patchiness of this ecosystem.

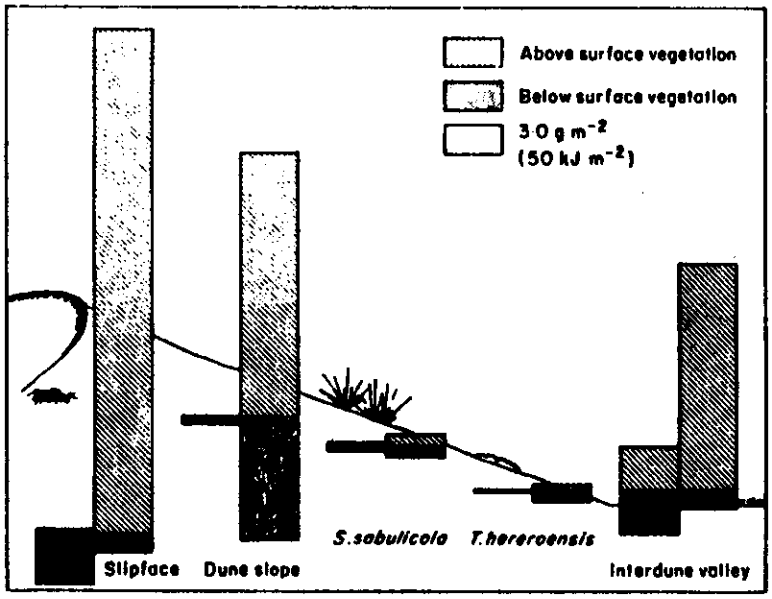

Figure 3. Effect of rain on biomass of vegetation (plants plus detritus) when each habitat and sub-habitat is evaluated separately. Left hand column represents biomass during dry year and right hand column during wet year in each case. Note high biomass within slipface habitat.

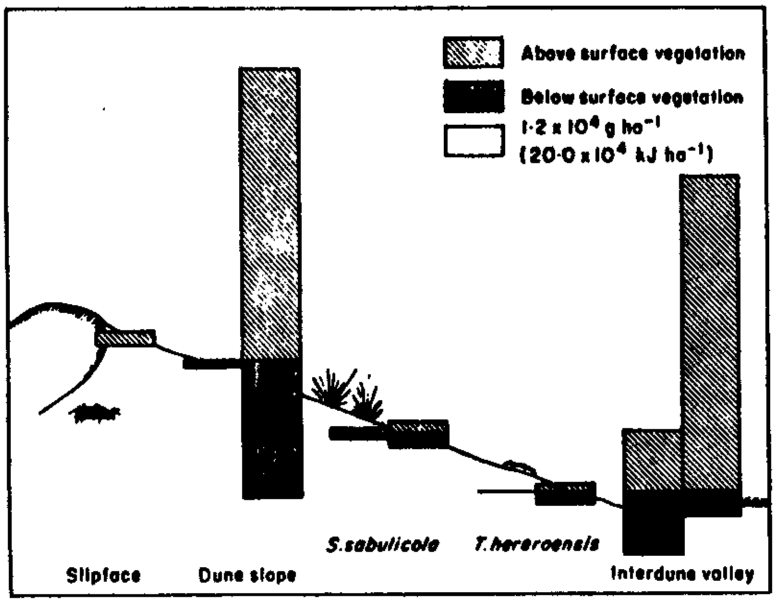

Figure 4. Effect of rain on biomass of vegetation (plants plus detritus) when adjusted for relative areas occupied by each habitat. Left hand column represents biomass during dry year and right hand column during wet year in each case. Note marked reduction in contribution of slipface from Fig. 3.

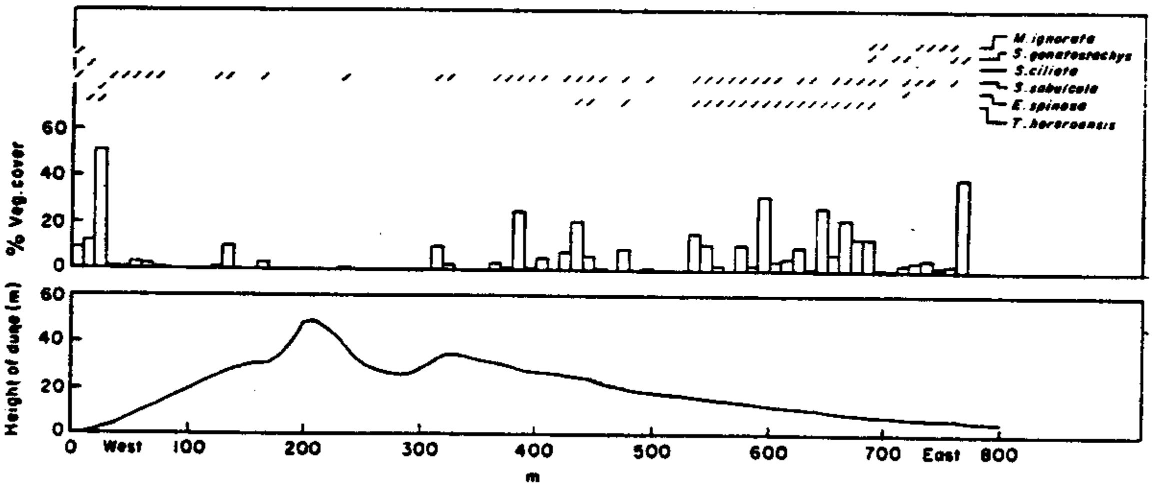

Figure 5. Distribution of the various plant species across a dune transect measured at 10 m intervals from one interdune valley on western side to adjacent dune valley on eastern side. Percentage vegetative cover is for all species combined. Note *inter alia* that *M. ignorata* is restricted to base of leeward side of dune where dune sand is coarsest and most stable. *Stipagrostis sabulicola* has most uniform distribution.

A statistical analysis of the changes in biomass brought about by rain within the various habitats and sub-habitats has been presented in Table 1. These data show that the variances were significantly different between the dry and wet periods. This is a result of the large degree of variation within samples which, in turn, is an expression of the extreme patchiness in the distribution of detritus and plants within the various habitats. A continuous transect across the breadth of one dune (Fig. 5) provides further evidence for the patchy distribution of plants across the dune slope and slipface habitat. Nevertheless, in view of the obvious practical difficulties involved in sampling in an ecosystem of this nature, the results are considered adequate for a first approximation.

Effect of rainfall on the distribution and biomass of animals

As expected, the distribution of animals within the dune ecosystem was found to be very patchy, reflecting the patchy distribution of the resource base. For example, *S. sabulicola* and *T. hereroensis* occupy less than 1 per cent of the dune slope surface, but 32 per cent of the animal life on the dune slopes is associated with these plants in a dry period and 29 per cent during a wet period. These results were obtained from the excavation method.

Table 2. *Effect of rain on various categories of the animal biomass in the three main habitats. Data obtained by excavation and transect census*

Habitat	Biomass(g m^{-2}) (dry year)	Biomass (g m^{-2}) (wet year)	Change (%)
Interdune valley			
Carnivores	0·0056	0·0001	
Herbivores	0·0065	0·0017	
Omnivores	0·0024	0·0155	
	Σ 0·0145	0·0173	+19
Dune slope			
(Includes *T.h.* & *S.s.*)			
Carnivores	0·0055	0·0168	
Herbivores	0·0009	0·0164	
Omnivores	0·0016	0·0658	
	Σ 0·0080	0·0990	+1138
Slipface			
Carnivores	0·0032	0·0026	
Herbivores	0·0018	0·0212	
Omnivores	0·0894	0·3212	
	Σ 0·0944	0·3450	+266
Whole ecosystem			
Carnivores	0·0056	0·0075	
Herbivores	0·0040	0·0084	
Omnivores	0·0029	0·0474	
	Σ 0·0125	0·0633	+406
Ratio			
Carnivores/herb. and omn. (whole ecosystem)	1 : 1·23	1 : 7·44	

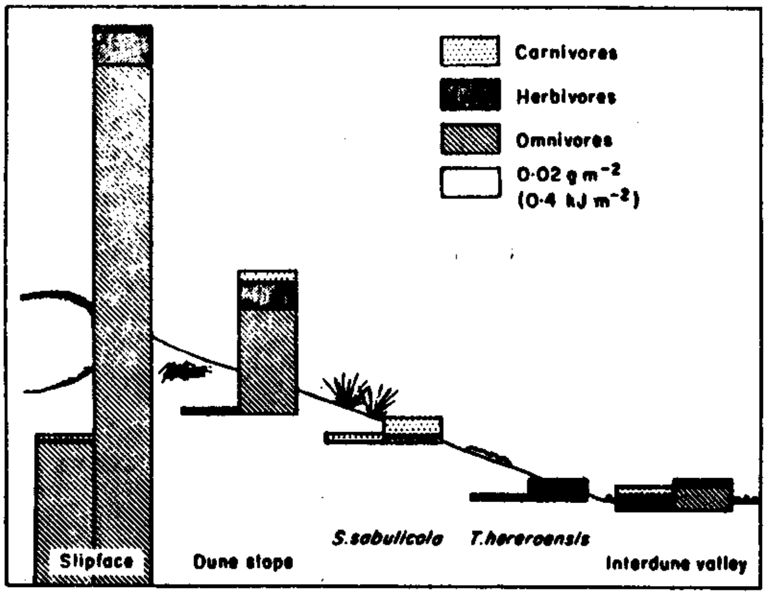

Figure 6. Effect of rain on animal biomass when each habitat and sub-habitat is evaluated separately. Left hand column represents biomass during dry year and right hand column during wet year. Note high biomass of slipface.

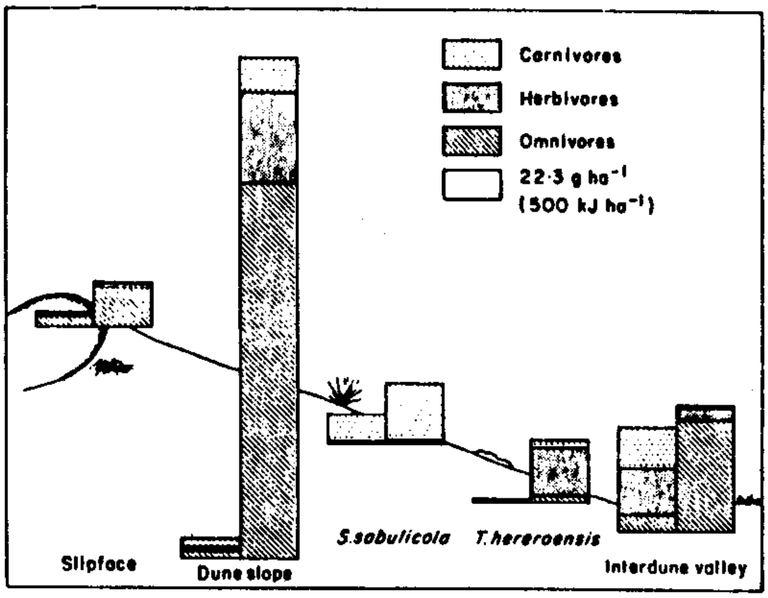

Figure 7. Effect of rain on animal biomass when adjusted for relative areas occupied by each habitat. Left hand column represents biomass during dry year and right hand column during wet year. Note marked reduction in contribution of slipface from Fig. 6.

On the slipface during the wet period 80 per cent of the animals excavated were located at the base of the slipface, an area which constitutes only 10 per cent of the total slipface. Although we have no comparable measure in the interdune valley, the spatial distribution of animals is probably most homogeneous in this habitat in accordance with the more uniform distribution of the vegetation.

Two methods, excavation and transect censuses, were used to estimate the biomass of the animals in the various habitats. The habitats and sub-habitats which contained the greatest number of species were: slipface (21), *T. hereroensis* (48) and *S. sabulicola* (22). The biomass data do not, however, follow the same pattern and are presented in Table 2 and Figs 6 and 7.

In Table 2 the values obtained for the sub-habitats (*T. hereroensis* and *S. sabulicola*) have been combined with those for the dune slope. On this basis the increase in animal biomass after rain on the dune slope was 1·138 per cent, 266 per cent in the slipface habitat and 19 per cent in the interdune valleys. For the entire ecosystem the overall increase in animal biomass was 406 per cent.

Figure 6 shows that when the animal biomass is evaluated separately for each habitat, the slipface is the most productive followed by the dune slope and then the interdune valley. When the biomass is adjusted, however, for the relative area occupied by each habitat (Fig. 7), then the dune slope is by far the most productive followed by the interdune valley, then the two sub-habitats and finally the slipface. Of special interest in this respect is the small contribution of the slipface fauna to the whole ecosystem, in spite of the high concentration of animals per unit surface area.

The data contained in Figs 6 and 7 also illustrate the relative importance of omnivores in most of the habitats during both the dry and wet periods. Exceptions to this generalization are the two sub-habitats (*T. hereroensis* and *S. sabulicola*) which support mostly herbivores and carnivores respectively. Also, during the dry period the biomass of omnivores was relatively low in the interdune valley but became the predominant type during the wet period. The general preponderance of omnivores is probably a reflection of the opportunistic feeding behaviour of the fauna.

Discussion

Effect of rainfall on total biomass and productivity

Vegetation

The productivity of some of the world's deserts has been reviewed by Noy-Meir (1973, 1974) and more recently by Hadley (1979). These summaries indicate that the annual net primary production of above-ground vegetation varies from 30 to 200 g dry weight m^{-2} in arid zones. More specifically, Soholt (1973) has reported a net primary productivity of *ca.* 31 g m^{-2} yr^{-1} in the Mojave Desert and Whittaker & Niering (1975) 92–105 g m^{-2} yr^{-1} for two desert sites at the base of the Santa Catalina Mountains in Arizona. The lowest figure reported is 16 g m^{-2} yr^{-1} for an IBP desert site in the southwestern United States (Webb *et al.*, unpubl.).

In the present investigation we did not measure primary productivity *per se* but Noy-Meir (1973) has argued that the type of vegetation present in the ecosystem determines the ratio of biomass to production. For example, in a community dominated by drought-resistant deciduous shrubs, 20–40 per cent of the biomass of 150–600 g m^{-2} is due to annual production. In contrast, in communities dominated by annuals the annual production of both roots and shoots is equivalent to the standing crop. Therefore, even if we allow a 100 per cent turnover rate in the Namib dune system, the total biomass of plants below and above the surface during a dry period only amounts to 5·7 g m^{-2}. Consequently both biomass and productivity in the Namib dunes represent the lowest figures reported to date. Moreover, if the importance of the two perennial plants *T. hereroensis* and *S. sabulicola* as a percentage of the total biomass of plants is considered, then the ratio of productivity to biomass is likely to be far below 100 per cent thus emphasizing the extremely low productivity of this dune system.

As Hadley (1979) has pointed out, information on subsurface productivity is scarce and he reports one set of data (100–400 g m^{-2} yr^{-1}) for arid zones in general. Again, even allowing for a 100 per cent turnover rate in the Namib dunes, our biomass figure of 2·99 g m^{-2} for a dry period is the lowest reported to date.

Figure 8 illustrates the profound effect of rain on the dune system. The biomass of surface plants increased nine fold, surface detritus 208 fold, subsurface plant material 2·5 fold and subsurface detritus 1·6 fold. After rain, plants and detritus still constituted the same proportion of the total biomass of vegetation as during the dry period, 92–94 per cent and 8–6 per cent, respectively.

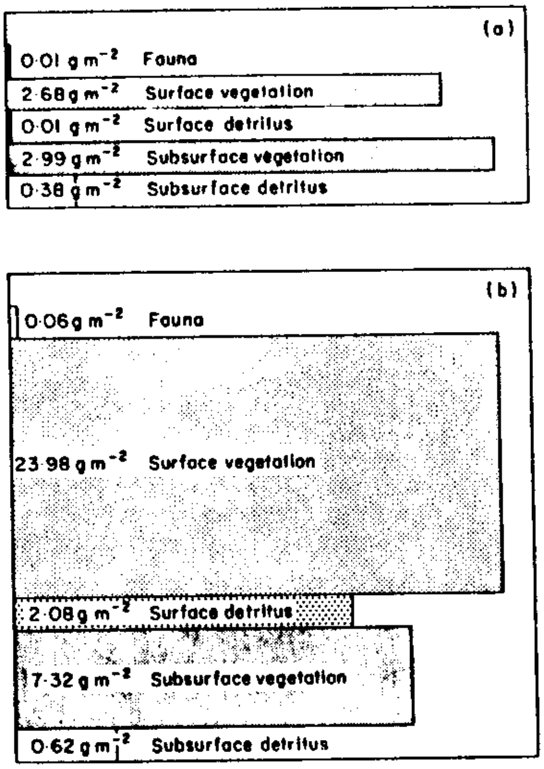

Figure 8. Biomass of plants, detritus and animals on entire ecosystem basis for a dry year (a) and a wet year (b).

The dramatic increase in above-ground detritus following rain can probably be attributed to three factors. First, the production of ephemeral grasses was increased by the rain. Second, the vegetation cover on the dune slopes also increased and this served to trap much of the wind-blown detritus. Otherwise it would have been rapidly buried on a shifting slipface. Third, the time interval (10 months) between sampling and the rainfall event was probably too short to allow extensive burial of the detritus which would otherwise have been beneath the shifting sands. The last reason would also explain the relatively small increase in subsurface detritus.

Root/shoot ratios

The extreme aridity of desert soils has frequently led to the assumption that the ratio of roots to shoots would be greater in desert plants than in temperate ones. This has, however, not always been confirmed by actual measurement. For example, Orians & Solbrig (1977) have reported great variation in root/shoot ratios in desert plants. Also Noy-Meir (1973) states that root/shoot ratios for winter-active desert annuals (0·2–0·5) are not much higher than in non-desert annuals. In a recent review Hadley (1979) concludes that ratios for below-ground/above-ground biomass are more closely related to plant life forms or temperature regimes than to aridity, and that the ratios can vary from 16 to 20 in perennial grasses and from 1 to 3 in arid-adapted shrubs.

In the present study the below-ground/above-ground plant biomass ratio was 1 : 0·9 during the dry period and changed to 1 : 3·3 after rain. These data reflect the predominance of the perennial plants, with their more extensive root systems, during the dry period and the relatively luxuriant above-ground growth of ephemeral grasses during the wet period. When the root/shoot ratios are evaluated within the separate habitats during the wet period the following ratios are obtained: interdune valley—1 : 11·7; dune slope—1 : 2·04. These results again reflect the preponderance of ephemeral grasses in the interdune valley and the importance of robust perennial plants on the dune slope. This is further confirmed by the observation that the root/shoot ratios of the long-lived perennials, *T. hereroensis* and *S. sabulicola*, did not change significantly from the dry to the wet period.

Animals

The animal biomass of 0·01 g m^{-2} during the dry period, as in the case of the plant biomass, is the lowest figure reported to date for any terrestrial ecosystem. The rainfall event resulted in a six fold increase of the animal biomass and the significance of these data will be discussed under the heading: energy, water and nitrogen cycles.

Effect of rain on the biomass and relative stability of the separate habitats

When stability is evaluated on the basis of change in biomass of the biota within separate habitats from the dry to the wet period, the interdune valley appears to be the most stable of the habitats. The plant biomass increased 2·7 fold in the interdune valley, 9·4 fold on the slipface and 53 fold on the dune slope. The animal biomass increased very slightly (1·2 fold) in the interdune valley from the dry to wet period. Although this increase is probably influenced by sampling error, the data suggest that animal populations are more stable in this habitat than in the remaining two which showed an increase in animal biomass of 7·7 fold (slipface) and 17·4 fold (dune slope).

Why this great difference in degree of stability of the populations in the various habitats? Differences between the interdune valley and dune slope may be attributed to the physical characteristics of the substrate. Apparently the interdune valley soils have a lower water storage capacity as evidenced by the observation that the same species of grass grow into much larger specimens on the lower dune slope than in the neighbouring interdune valley. The vegetation of the interdune valley therefore develops very rapidly after rain, sets seeds and dries into what may be described as a naturally cured hay. The grass species involved are predominantly *Stipagrostis gonatostachys* with *S. ciliata* growing in more stoney areas. The fauna of this habitat is, however, somewhat less stable than the vegetation, although evidence for this conclusion was not derived from the present study. For example, after sufficient rain several tenebrionid species, which only occur in the interdune valleys, will erupt in great number (10 per m^2) after being totally absent from the surface since the previous rain.

In contrast, the dune slope only supports the two perennial plants (*T. hereroensis* and *S. sabulicola*) during a prolonged dry period. After sufficient rain an extensive ephemeral vegetation develops rapidly which accounts for the relatively high instability of this habitat. In addition, certain species of weevils (*Leptostethus*) are entirely absent from the dune slope for years during prolonged dry periods, only to erupt after sufficient rain and the concomitant increase in vegetation. Although this vegetation cover may persist for several years it should, nevertheless, be considered quasi-ephemeral in comparison to the permanent species of the dune slopes.

The stability of slipface populations is intermediate when compared with the interdune valley and dune slope. Its vegetation consists entirely of wind-blown detritus except in rather rare instances when wind causes the sand of the slipface to advance over living plants, growing at the slipface base. The stability of the resource base in this habitat is therefore controlled by the influx of detritus from the other two habitats, where plants grow. The growth of ephemeral grasses after good rains will therefore eventually influence the accumulation of detritus on the slipface and consequently the stability of its animal populations. Because of the relatively stable resource base, provided by accumulated detritus, the slipface fauna is reasonably stable with respect to time. Although there is an increase in response to good rains, the population decline thereafter is very gradual. This is in contrast to those tenebrionid species, dependent on living plants in the other habitats, which decrease in number as precipitously as they increase after sufficient rain.

Effect of rain on distribution patterns of plants and animals

Another conclusion to emerge from this study is the tendency towards a more homogeneous distribution of resources with increased precipitation. During the dry period the lack of vegetation on the dune slope limited the activity range of those species foraging either on concentrations of detritus or on growing plants. Following the growth of the extensive ephemeral plant cover in response to good rains, animals mainly confined to the slipfaces, the Nara plants on the edge of the dune ecosystem, or the riverbed bordering the dune ecosystem, expanded their foraging range into the dune slope habitat. These include the tenebrionid species *Onymacris laeviceps* from the slipface, *O. plana* from the Nara plants

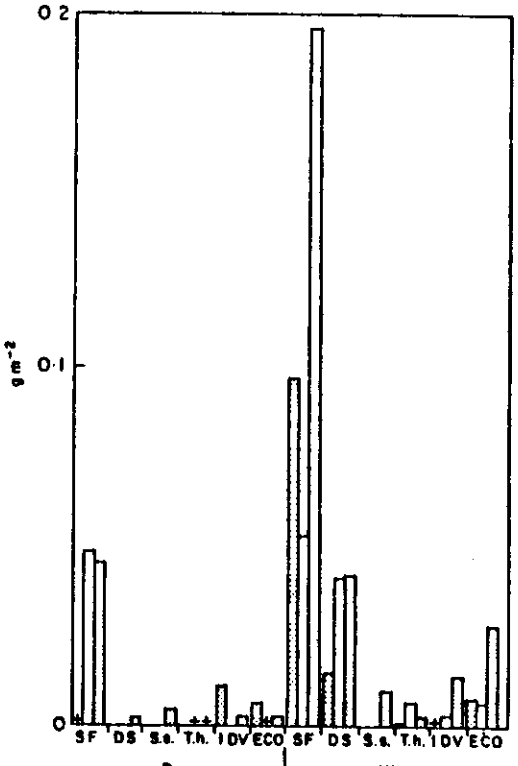

Figure 9. Effect of rain on distribution of animal biomass (g m^{-2}) in terms of category of activity within the various habitats of the dune ecosystem. Animals which are active and feed only on the surface are indicated by coarsely-shaded columns, those which are active and feed only below the surface by unshaded columns and those which feed on surface but live mostly below the surface by finely-shaded columns. Slipface (SF), dune slope (DS), *S. sabulicola* (S.s.), *T. hereroensis* (T.h.), interdune valley (IDV), entire ecosystem basis (ECO). When biomass is too small to portray graphically the symbol (+ +) is used.

and *O. rugatipennis* from the riverbed. At the same time there was a general tendency for the increased populations of common tenebrionid beetles to range into the adjacent habitats, whereas during the dry period they were more localised. The gemsbok *Oryx gazella* also returned to the dune system, grazing preferentially on the ephemeral *Asthenatherum glaucum*. Other animals, e.g. the lizard *Meroles cuneirostris*, that were previously concentrated about the perennial plant species, both for foraging and for ease of thermoregulation, expanded their range to include the ephemeral plant species. Gerbils and other dune animals were also observed to extend their ranges and thus there was an overall expansion of niche occupation from the dry to the wet period.

One species of interdune grass, *Stipagrostis gonatostachys*, also evinced this broadening of niche. *S. gonatostachys*, endemic to the Namib dune ecosystem, occurs in the interdune valleys where the occasional rain of approximately 20 mm causes germination. With the unusual amount of rain early in 1976, the sand of the dune slopes was sufficiently wet to induce germination there as well. This response was not observed in the other interdune valley species, *S. ciliata*, which, although having a much wider geographic distribution, is not the extreme opportunist that *S. gonatostachys* apparently is.

Location of feeding activity as well as other activities of the fauna (Fig. 9) was restricted to three definite categories, those that live and forage entirely within the sand medium, those that live and forage above the surface and those that feed above surface but pursue other activities both on and in the sandy substrate. Larvae of the tenebrionid beetles comprise a significant proportion of the first category, in which are also included other larval forms and legless lizards. In the second group are many of the small herbivorous insects associated with the perennial *T. hereroensis*, as well as birds, the larger, more mobile mammals, e.g. the hare and the oryx, and the larger reptiles, e.g. *Chamaeleo namaquensis*. The smaller animals can thus use the plants as a refuge when sand surface conditions become unsuitable while the larger ones in this category must tolerate the ambient conditions. The most commonly used activity pattern is that employed by the numerically dominant tenebrionid beetles of the slipface and dune slope. These animals forage on the surface where the detritus is continually being redistributed and made available by the wind, but can escape into the sand when surface conditions become unfavourable. Dune lizards and geckos, the side-winder, solifuge and spider species, silverfish and the dune gerbils all show this activity pattern. Figure 9 includes all animals encountered during excavations and transect censuses and thus includes such temporary dune inhabitants as the grey-backed finchlark. When the latter are excluded from the analysis the proportion of those species that forage on the surface but escape into the sand becomes higher and it is clear from Fig. 9 that they were the dominant group both during the dry and wet periods. Their dominance, particularly on the slipface was, however, significantly enhanced by rain.

Energy, water and nitrogen cycles

The finding that a large proportion of the primary production in the Namib dune ecosystem is utilised by invertebrate consumers is not unexpected. A similar situation exists in other deserts. For example, Schumacher & Whitford (1976) indicated the importance of ants as primary consumers in the Chihuahuan Desert where they are the most numerous insects present with the possible exception of termites. Similarly Burkhart (1978) has shown that the alkali grasshopper *Anconia integra* removed a total amount of vegetation from a salt bush community equal to 5·2 per cent of the net primary productivity but that only half of this was actually consumed.

As far as desert vertebrates are concerned, herbivorous lizards appear to be unimportant consumers of the primary production (Nagy & Shoemaker, 1975). Likewise, consumption by Merriam's kangaroo rat (*Dipodomys merriami*) was only 1·2 per cent of the total net primary production in southeastern Arizona and 6·9 per cent of the total net production in the Mojave Desert (Chew & Chew, 1970; Soholt, 1973). In contrast, larger herbivores such as the jackrabbit appear to be able to metabolize 65 per cent of the energy contained in the spring annuals of the Mojave Desert (Shoemaker *et al.*, 1976) while Zervanos & Hadley

(1973) have shown that the collared peccary consumed 20 per cent of the annual production of prickly pear within their home range. The latter figure falls within the range of a 5–75 per cent consumption of the total primary production, which has been estimated for large domestic mammals grazing on arid vegetation (Whittaker & Niering, 1975).

Secondary consumption in desert communities is typically accomplished by spiders, scorpions, reptiles, small to medium-sized mammals, insectivorous birds and large raptorial birds (Hadley, 1979). In the same review Hadley reports that as many as 5–10 scorpions per m^2 can occur in warm North American deserts while spider density in a desert creosote community averaged 2·5 spiders per m^2.

To the best of our knowledge, however, the proportion of the primary production which is channelled through these various species and trophic levels has as yet not been quantified for any desert community. It is therefore difficult to make any exact comparisons, particularly for a dune environment. Nevertheless, there are certain obvious differences between the productivity and energy flow in a Namib dune system and other desert communities which have been studied. For example, in many deserts surface algae and the molluscs which consume them represent an important energy loop (Shachak & Steinberger, 1978). These organisms are entirely absent from the Namib dune ecosystem, probably due to the action of dry, hot wind-blown sand. Similarly, although lichens are an important component of the plant community of the western gravel plains of the Namib (north of the dunes), as they are in other deserts (Kappen & Lange, 1978), they are absent from the Namib dune ecosystem. Further comparisons reveal the absence of mammalian carnivores and large mammalian herbivores from the system under normal dry conditions. Moreover, although several species of scorpion have been found in the dunes, one apparently restricted thereto (*Protophthalmus holmi*), they are rare and would appear not to play the important role that they usually do in desert communities. The major difference, however, between the Namib dune ecosystem and other desert ecosystems studied to date is, first, the extremely low productivity and second, the slow degradation of accumulated detritus. The detritus provides an energy store for a relatively large variety of omnivores in the form of tenebrionid beetles and decomposition by microbial action is minimal. This relationship and the relationship between higher trophic levels in conjunction with water flows through the system will now be considered in some detail.

Energy and water flows

In Fig. 10(a),(b),(c) the major pathways of energy and water flux in the various habitats are illustrated.

In the interdune valley, rain of more than about 20 mm (cf. Seely, 1978*b*) causes germination of the two ephemeral grass species *Stipagrostis gonatostachys* and *S. ciliata*. Either the rain or the appearance of the green grass triggers the eruption of several tenebrionids which are active on the surface only under these conditions, e.g. *Eustalopus octaseriatus* and *Pachynotelus* sp. They, along with other herbivores, feed upon the grass as long as it is green, and their populations decline as the grass withers. The grass dries and is turned into detritus by the sand-blasting action of the wind. Omnivores, using the detritus for energy and fog for moisture, continue living in the interdune valley, and, together with those herbivores able to use the dry grass, provide energy for the top of the trophic web.

During a prolonged dry period, roots persist in the interdune valleys because of the relatively stable substrate. Herbivores are important in the interdune valleys during the dry period. Presumably they either obtain moisture from fog dampening the material near the surface or perhaps metabolic water production is sufficient. Omnivores, using fog as a source of water, are also present in this habitat during the dry period.

The dune slope is the habitat where rain has its most dramatic effect. Increased soil moisture causes germination of both *S. sabulicola* and *T. hereroensis*. In addition, three species of grass, with growing periods of several years or less, germinate, viz. *A. glaucum*, *E. spinosa* and *S. gonatostachys*. The ephemeral species grow as long as the soil moisture is adequate, then wither and become detritus through wind-action. The two perennial species

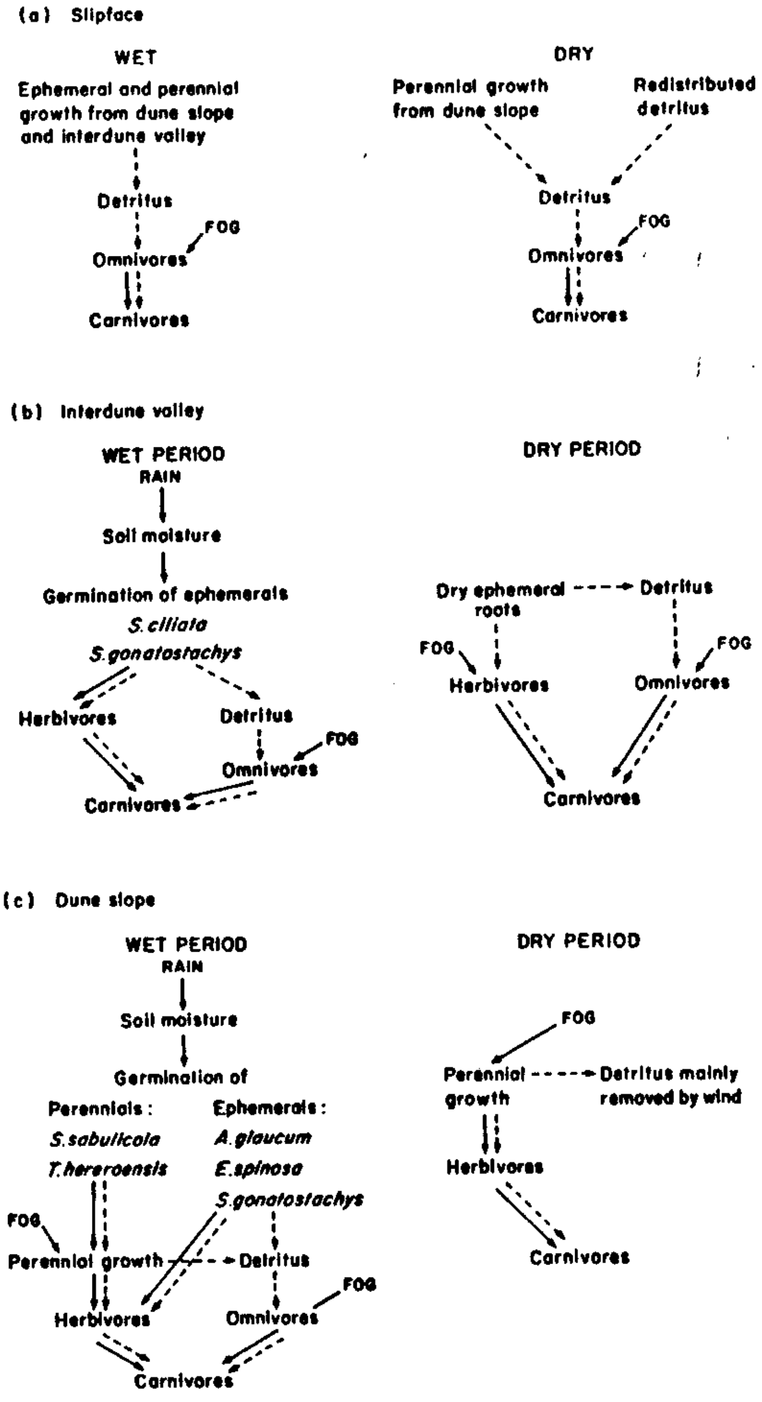

Figure 10. A comparison of the flow of nutrients and water within the major dune habitats, during a dry and a wet year: (a) slipface, (b) interdune valley and (c) dune slope; nutrients (- - - -), water (——).

continue growing, with fog supplementing the available soil moisture, and producing detritus as parts die off. As in the interdune valley, energy is thus available for all three consumer groups during a wet period. During the dry period, the ephemeral growth is absent, having been reduced to detritus and removed from the dune slope habitat by the wind. Because of the instability of the sandy substrate, even the roots are blown away in time. A declining number of perennial plants continue to grow, with their water requirements supplemented by the fog. Omnivores are the least important animal component of the dune slope during a dry period.

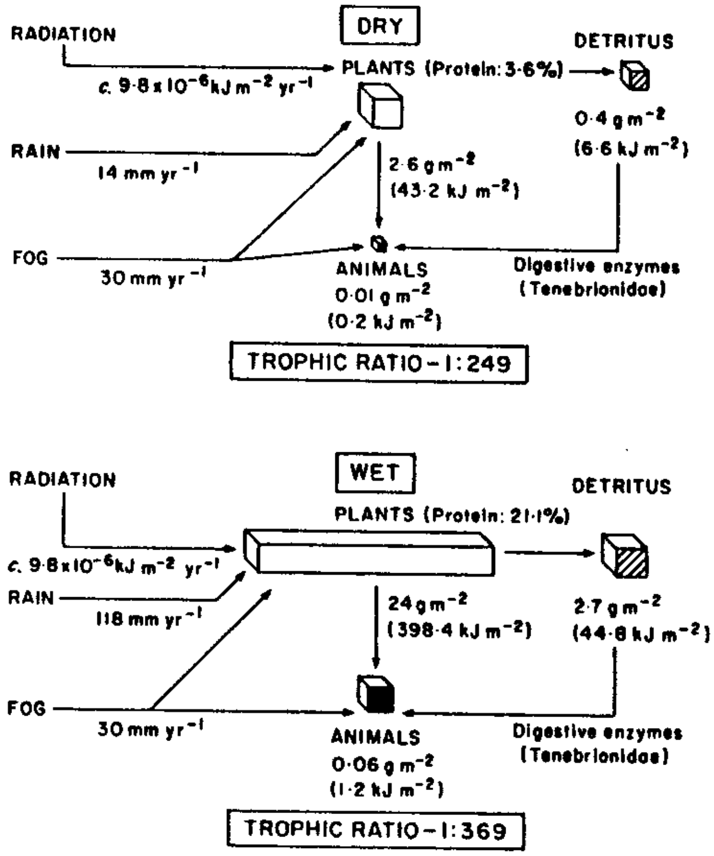

Figure 11. Flow of energy through a Namib dune ecosystem during a dry and wet year. Note large accumulation of detritus (litter), absence of microbial decomposition and importance of digestive enzymes in beetles for recycling energy in detritus. The low protein content of detritus during dry periods may be an important limiting factor.

On the unstable slipface vegetation does not germinate even in the event of adequate rainfall. Vegetation appearing to grow on the slipface is usually on that part of the dune slope in the process of being covered by the advancing cascade of sand. However, good rainfall does have a marked effect on the slipface. The detritus increases dramatically and, using fog as the source of free water, the omnivores increase also. Some of the detritus is buried by the sand and wind and this energy source is stored beneath the surface until the wind again uncovers it. During a dry period the fresh input of energy in the form of detritus decreases and the relative contribution from redistributed detritus increases. Omnivores continue to flourish here, decreasing in numbers as the source of energy diminishes. The detritus necessary to support the fauna in this habitat need not originate in the immediate area but may be transported from some distance. Thus, the fact that the Namib dune ecosystem is surrounded on three sides by an ephemeral grassland may contribute to maintaining detritus levels in the slipface habitat (Robinson & Seely, 1980).

The gross flow of energy through the entire ecosystem has been illustrated in Fig. 11. These figures are based on a combination of all survey methods employed in the study and the mean values obtained for the energy content of the vegetation and the animals, 16·6 kJ g^{-1} and 20 kJ g^{-1}, respectively. Examination of Fig. 11 reveals that during both a dry year and a wet year the radiation intensity is high but the resulting biomass is extremely low.

The increase in the energy of the plant biomass from 43·2 kJ m^{-2} to 398·4 kJ m^{-2} after rain represents a marked ninefold increase, while the increase in the energy of the detritus from 6·6 kJ m^{-2} to 44·8 kJ m^{-2} represents a sevenfold increase. Similarly, rain increased the energy contained in the animal biomass sixfold. Therefore, when allowing for inevitable sampling errors, the magnitude of increase in all three components was similar. Also the energy contained in the detritus as a percentage of the total energy in both plants and detritus was 15·4 per cent during the dry period and 11·3 per cent during the wet period. Again, these figures are similar but the results may also reflect a lag in detritus formation from living plants.

The transfer of energy from plants to detritus is a result of two processes which are inherent in the dune ecology, namely the short ephemeral life of the dune grasses and the sand-blasting action of the surface winds. Once the detritus is formed it creates an important energy resource which can be slowly utilized by the primary consumers. To illustrate this importance we can compare the trophic ratio between the energy contained in the animal biomass with that contained in the detritus during both the dry and the wet periods. This comparison shows a trophic ratio of 1 : 33 during the dry period and 1 : 37 during a wet year. It should, however, be borne in mind that the animal biomass used in the above calculations did not consist entirely of primary consumers and that, as a result of the comparatively short interval between the rainfall event and the second sampling period, considerably more plant material was still available for detritus production. These data suggest that detritus represents an important energy store for the primary consumers.

When we compare the ratios between the energy contained in the animal biomass with that contained in the total vegetation (plants and detritus), the comparison reveals a trophic ratio of 1 : 249 in the dry period and 1 : 369 in the wet period. These trophic ratios are very wide, even when compared with a ratio of animal biomass to leaf biomass of 1 : 123 established for a tropical rain forest (Odum *et al.*, 1970). Obviously, however, all the energy contained in the plant biomass is not available to the animals. For example, our field observations have shown that the intensity of herbivory on *T. hereroensis* and *S. sabulicola* is not great. The former plant is protected by high oxalic acid concentrations and the latter is very fibrous with tightly rolled spikey leaves. These characteristics contribute in part to their long survival in the dune habitat. Nevertheless, the seeds of *T. hereroensis* are eaten by the sand-diving lizard *A. anchietae* (Robinson & Cunningham, 1978), the leaves have been found in the burrows of the rodent *Gerbillurus paebae* and *Oryx gazella* have been observed to consume entire individual plants. Similarly, after rain the fresh new shoots of *S. sabulicola* are eaten by gemsbok *O. gazella* and other animals including weevils. We conclude therefore that the wide trophic ratios established for this dune system mean that a large surplus of energy is available to the omnivores and herbivores but not necessarily for the carnivores at a higher trophic level. This surplus would then be available for slow consumption during prolonged periods of minimal rain.

Nitrogen

Chemical analyses of the dune sands have revealed that all three macro plant nutrients, phosphates, potassium and nitrogen are in short supply. The lack of nitrogen is aggravated by the absence of any legumes from the plant community. During a dry period the crude protein percentage in detritus ranged from 2·3 to 4·8 per cent with a mean of 3·6 per cent ($n = 9$). In contrast, the crude protein percentages of ephemeral grasses after rain ranged from 16·3 to 26·5 per cent with a mean of 21·1 per cent and when only the leaves of the ephemeral grass *Asthenatherum glaucum* were analysed a percentage of crude protein as high as 37·4 per cent was obtained.

Even allowing for the inherent errors of the Kjeldahl technique which was used to estimate crude protein in this study, the differences between the protein content of food available to the animals before and after rain is very marked indeed. It would appear then as if the primary consumers of the dune system may be faced with a protein deficiency during prolonged dry periods. In view of the high protein content of animal tissue the carnivores would not have to contend with the same problem, but available energy may be limiting in the case of the carnivores because of the close ratios obtained between carnivores to herbivores plus omnivores, in both dry and wet periods (1 : 1·23 and 1 : 7·44 respectively).

Food web

In a review on the productivity of desert ecosystems Hadley (1979) concludes that complex food webs rather than simple food chains exist in natural desert communities. Based on our field observations over 10 years and other criteria, we have drawn a generalised food web (Fig. 12) and examination of this web supports Hadley's conclusion. For example, the energy eventually consumed by one of the top carnivores, the side-winding adder, *Bitis peringueyi*, is ultimately derived from energy in the detritus and to some extent in the plants. This energy passes through aphids, bugs, grasshoppers, termites, lepisma and small tenebrionids to reach the two sand-diving lizards *M. cuneirostris* and *A. anchietae* which are the main prey items of the side-winder.

For the sake of clarity only major prey/predator relationships have been included in Fig. 12. Nevertheless, it is clear that while most of the animals lower down on the food chain are dune endemic or at least resident species, most of the higher predators are regular or irregular visitors to the dune environment. In fact, all of the larger animals leave the dune ecosystem entirely during prolonged dry periods. Thus the conspicuous adult forms of the larger tenebrionid beetles in particular are almost free from predation during the dry

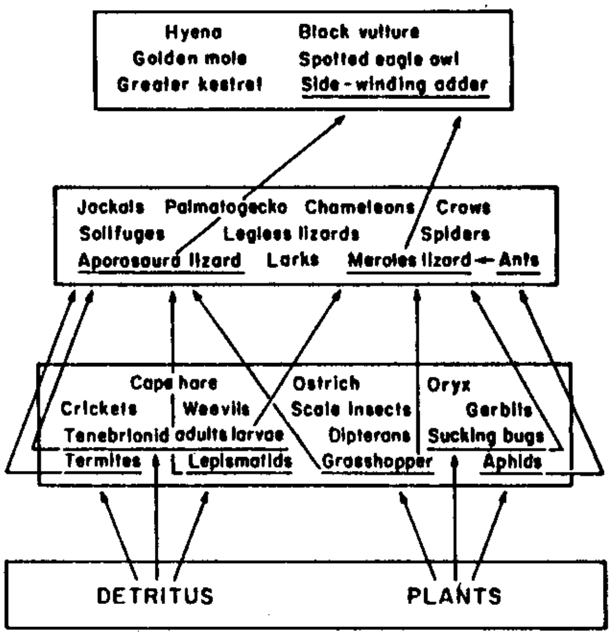

Figure 12. A generalized scheme illustrating the flow of energy and other nutrients through the animals of the dune ecosystem. In view of the marked degree of opportunism and overlap exhibited in the feeding activities of the fauna, only one major food web, ending in *Bitis peringueyi*, the side-winding adder, has been indicated.

period. When examining Fig. 12 it should be remembered that within the study area tenebrionid beetles are the most common dune endemic group with a minimum of 23 species occurring. Minimum values for the other groups are: other identified insects, 9 species; weevils, 4 species; arachnids, 11 species; reptiles, 6 species and birds and mammals, one species each.

Detritus and decomposition

As a result of the aridity of desert soils, litter tends to accumulate on the surface and can in fact exceed above-ground living biomass (Hadley, 1979). Microbial decomposition of the litter is retarded by the low moisture levels in the soil and consequently large amounts of energy can be made available to detritus-feeding arthropods. For example, Johnson & Whitford (1975) have estimated that subterranean termites can consume as much as 50 per cent of the net productivity in certain Chihuahuan Desert sites. Millipedes on the other hand were found to utilise only 0·2 per cent of the net primary production of a Chihuahuan Desert community (Crawford, 1976). Similarly, Shachak *et al.* (1976) have demonstrated that the isopod *Hemilepistus reaumuri* consumed between 1·1 and 4·3 per cent of the available plant material annually in the Negev Desert.

The Namib dune system, as discussed previously, fits this pattern well. Although our methods did not allow us to estimate that percentage of net primary production which detritus comprises, examination of the biomass figures for detritus and plants (Fig. 11) shows that it would be very high. This is not surprising in view of the low bacterial counts established for the hot, dry shifting sands of the dune system (le Roux, 1970). A most unusual feature of decomposition in the Namib dunes, however, is the fact that the bulk of the detritus is consumed by tenebrionid beetles and not by termites, isopods or millipedes. The latter two groups are completely absent from the dunes. Moreover, decomposition of the cellulose-rich detritus is not accomplished by microbial enzymes but apparently by endogenous cellulases which have been found in the digestive tracts of these beetles (Marcuzzi, 1977*a*,*b*).

This phenomenon therefore permits the accumulation of great pads of detritus both above and below the sand surface (Plate 4). This detritus is slowly consumed as it is recirculated by the prevailing winds, particularly through the slipface habitat. It is this slow release of detritus that provides the energy for the continued existence of the fauna on the vegetationless slipfaces, while condensed fog moisture provides the necessary water.

Opportunism and flexibility

In view of the fluctuating and unpredictable nutritional plane which desert animals are exposed to, they are typically opportunistic in their feeding behaviour (Noy-Meir, 1974). This opportunism is not restricted to switching from one energy source to another as the one becomes depleted, but also includes the selection of specific plants to meet specific physiological needs. This principle is well illustrated by the findings of Burkhart (1978) who has shown that the alkali grasshopper, *Anconia integra*, shifts its food preference from *Atriplex canescens* to *Suaeda torreyana* during hot summer months in the Sonoran desert to provide a more concentrated source of energy and water.

The Namib dune fauna is no exception to this rule and exhibits marked opportunism and flexibility in behaviour and feeding (Plate 5). Most of the known adaptations are behavioural in nature, allowing the animals to take advantage of irregular and unpredictable events such as rain and fog. Extreme temperatures are avoided by burrowing beneath the sand. Although each beetle species has a general foraging time, this can be entirely reversed by the occurrence of strong winds which redistribute detritus on the slipface. Surface feeding time of the lizards is entirely dictated by temperature (Robinson & Seely, 1980). To take advantage of the advective fogs, the tenebrionids are on the surface at times and temperatures when they would normally be below the surface (Hamilton & Seely, 1976; Seely & Hamilton, 1976; Seely, 1979). The tenebrionids feed on detritus, seeds, green plants, dry or fresh carrion or even living animals when the opportunity arises. The slipface lizard (*A. anchietae*) consumes seeds or insects as available. All of the omnivores are relatively long lived. Beetles have been recorded as living for over one year in the field and several years in the laboratory. Slipface lizards live for over three years in the field (Robinson, pers. comm.). Thus the dune endemic species, particularly the numerically dominant tenebrionid beetles, are extreme generalists that will shift temporal, spatial or feeding niche and overlap with other species as the opportunity arises. This high degree of behavioural flexibility presumably results from the instability of the climatic regime and the concomitant patchiness of the environment.

In contrast, most of the animals visiting the dune ecosystem do not have the flexibility to remain there indefinitely. Particularly the large grazers, e.g. oryx (*Oryx gazella*), and large predators, e.g. Lüdwigs Bustard (*Neotis ludwigii*) and black-backed jackal (*Canis mesomelas*), leave when conditions become unfavourable. Thus, although opportunistic in their use of the dune ecosystem, they do not have the niche breadth to become permanent dune residents.

Limiting factors

The most obvious limiting factor in any arid environment is water, so much so that Noy-Meir (1973) has suggested that a water flow model would be sufficient to represent the life processes of a desert ecosystem. Water *per se* is obviously important but it is also intimately related to many other essential life processes such as transport of soil nutrients, decomposition rates and therefore nutrient cycling which can all be considered as limiting factors. In reviewing the most important limiting factors Hadley (1979) includes water, nitrogen, phosphates and the slow rate of decomposition of litter following a short-term period of rapid growth, which exhausts nutrients faster than they can be replaced.

The Namib dune system again exhibits typical desert characteristics with respect to limiting factors. The marked increase in biomass which occurred after rain testifies to the great importance of water. The dramatic increase in nitrogen (protein) content of the plants is a reflection of the importance of water in mobilising this nutrient for protein synthesis by plants and its eventual utilization by animals. West & Skujins (1977) have commented on the fact that in certain cold North American semi-desert ecosystems only 12 kg N ha^{-1} yr^{-1} is taken up by new above-ground vascular plant growth. They also found that although blue-green algal components and cryptogamic crusts were able to fix large amounts of N, 70 per cent of this nitrogen was lost through volatilization and denitrification. In the Namib dune system significant algal components are apparently absent from the hot shifting sands and fixation of nitrogen by these organisms would appear therefore to be insignificant. Presumably the major source of nitrogen is derived from uric acid excreted by the dune fauna. Proliferation of the microbial components responsible for decomposition of this uric acid and the release of nitrogen to growing plants would be dependent on sufficient rain falling on the dunes. A relatively small percentage of the nitrogen taken up by ephemeral plants after rain would be returned fairly rapidly to the dune sand in the form of uric acid after passing through omnivorous tenebrionids. A larger percentage, however, would remain trapped in the detritus for many years as much of the ephemeral growth is reduced rapidly to detritus by the sand-blasting action of the wind.

As described previously, the very slow decomposition of litter or detritus in the Namib dunes retards nutrient cycling. Moreover, the ephemeral growth of grasses after rain is very rapid and must exhaust the available nutrients in the impoverished sands very rapidly. The latter conclusion was confirmed by the fact that a second high rainfall event, which occurred two years after the event described in this study, did not produce the same magnitude of response, although the total rainfall that fell was very similar (118 vs. 100 mm). In addition to the above factors, plant growth in the Namib dune system is also limited by the physical stability of the substrate which is characteristic for each habitat, as well as by the moisture holding properties of the various types of substrates. Hadley (1979) also reports that nitrogen is a key limiting nutrient in North American deserts and Charley & Cowling (1968) have found that phosphorus is limiting in certain arid regions of Australia, whereas we have found that the dune sands are deficient in both minorals.

As far as the limiting factors controlling the growth of animal populations are concerned, the previous discussion on energy and nitrogen cycling has shown that available energy does not appear to be a factor limiting the population growth of primary consumers. This confirms an hypothesis proposed by Noy-Meir (1978) for deserts in general. In contrast, the extremely low protein levels found in detritus and dead plants during a dry period suggests that this nutrient could quite possibly be an important limiting factor in the case of primary consumers. Nevertheless, as we proceed up the food chain, the relatively high proportion of carnivores on the one hand to omnivores and herbivores on the other (dry, 1 : 1·23; wet 1 : 7·4) suggests that there may be both a deficiency of energy and total protein at the higher trophic level of secondary consumption. In addition, it must be remembered that the extremely low biomass of animals means that the available energy and protein for secondary consumption is for the most part widely distributed over a large surface area. This wide distribution probably impairs predation and may well be an additional limiting factor in the case of secondary consumers.

A final limiting factor which should be considered is the availability of suitable habitats for both plants and animals. The extremely low biomass measured for this ecosystem suggests that available habitat is not a limiting factor and the findings of Robinson (pers. comm.) that a population of the territorial sand-diving lizard, *Aporosaura anchietae*, continued to double annually for three consecutive years during two high rainfall seasons would seem to confirm this. Nevertheless, if the rather specialized growing requirements of the perennial plant, *T. hereroensis*, at the base of the dune are considered, this may not be the case for all populations. Moreover, the dependence of certain animal species on isolated plants for shelter and thermoregulatory behaviour could well limit population size during prolonged dry periods.

Conclusions

The Namib dune ecosystem responds dramatically to rain. There is a ninefold increase in the potential energy contained in the plant biomass following rain, a sevenfold increase in the potential energy contained in the detritus biomass and a sixfold increase in the potential energy of the animal biomass. Rain also causes an expansion of the niches occupied by certain animals and plants to the extent that overlap occurs in specific instances. Similarly, rain reduces the extreme patchiness in the distribution of both plants and animals by increasing the uniformity in the distribution patterns of most species.

The various habitats within the dune ecosystem differed markedly in both productivity and stability. The dune slope is the most productive after rain and the least stable, while the interdune valley is the most stable habitat and the second most productive after rain, in terms of contribution to the total biomass of the ecosystem as a whole. However, when the individual habitats are evaluated separately the slipface supports the richest biomass of vegetation and animals; the vegetation being entirely in the form of detritus.

The dune ecosystem is similar in many ways to other desert communities that have been studied. For example, availability of potential energy does not seem to be a limiting factor, while water and plant nutrients such as nitrogen and phosphorus are key limiting factors in the productivity of the ecosystem. These factors are aggravated by the instability of the substrate within certain habitats of the dune system.

The Namib dunes do, however, differ in degree from other desert ecosystems in several respects. Because of the action of dry wind-blown sand there is a very pronounced accumulation of potential energy in the form of detritus in the dunes. Microbial decomposition of this energy resource is almost absent and the recycling of this cellulose-rich material is largely accomplished by a variety of tenebrionid beetles and more specifically by endogenous cellulase enzymes in their digestive tracts. The continuous redistribution of this energy source by wind thus provides a slow release of energy to support a surprisingly complex food web on dunes which are almost without vegetation. The very low protein content of the detritus, however, probably limits the growth and reproduction of the herbivore and omnivore populations which feed upon it. Finally, the biota of this ecosystem exhibit unique ecophysiological and behavioural characteristics such as fog imbibition, fog basking and water storage which enhances their opportunism and flexibility in exploiting irregular pulses of food and water in this unusual ecosystem.

The surveys involved in this investigation would not have been possible without the enthusiastic help of a team of field asistants, frequently working under difficult conditions. The team included: B. Anderson, M. Bester, S. Britten, G. Cloete, R. Crawford, K. Cuthbert, L. Davis, M. Gericke, J. Jurgens, A. J. Lintvelt, D. Mostert, K. O'Brien, B. Oelofsen, E. Pfeifer, L. Powrie, K. Rogers, A. Suttle, W. Veith and J. Venter. We are especially grateful to Kate O'Brien and Walter Veith for their assistance in the laboratory and with data reduction. M. D. Robinson and N. F. Hadley kindly commented on a draft of this manuscript. Financial support was provided by the CSIR, Transvaal Museum and the Universities of Stellenbosch and Cape Town. The Division of Nature Conservation and Tourism, SWAA, provided facilities and permission to work in the Namib–Naukluft Park.

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(b)

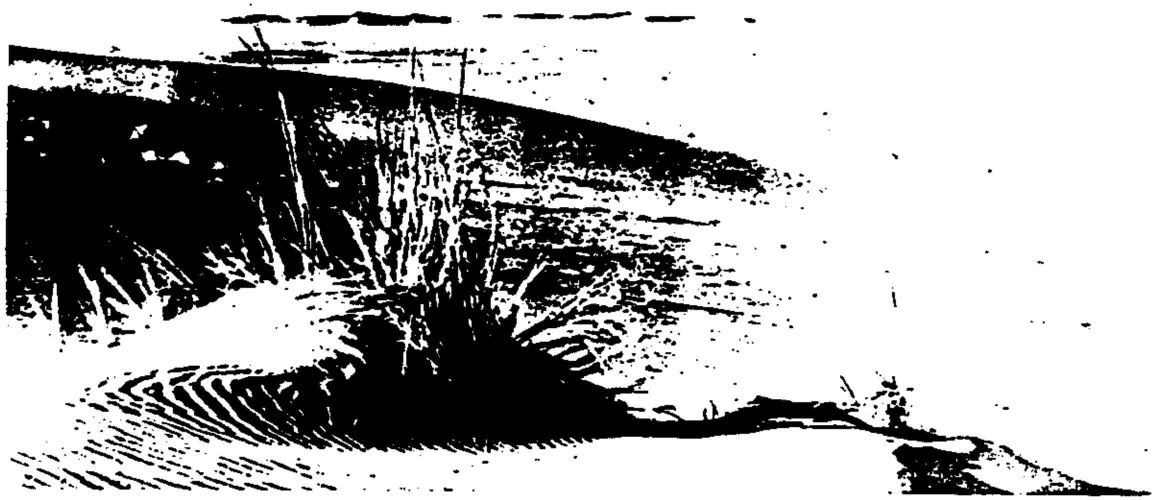

Plate 3. Two sub-habitats, created by the perennial plants *Trianthema hereroensis* (a) and *Stipagrostis sabulicola* (b) on the dune slope, were evaluated separately during most of the surveys.

(See caption overleaf)

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