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Physical and biotic environments of the southern Namib dune ecosystem

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The sand dune ecosystem of the Namib Desert of southwestern Africa contains a species-rich and highly endemic biota. As a first attempt to understand the evolution and ecology of this ecosystem, a number of abiotic and biotic characteristics are described and quantified, and the causal relationships between 18 of these variables are compared. Wind and dune morphology affect 16 of the 18 environmental parameters and are therefore considered major environmental factors in this ecosystem. Organic detritus cycles, fog moisture, soil temperature and sand grain size also have had important direct or indirect influences on the evolution of the dune biota. Four distinct biotic communities are defined and described for the north-central portion of the southern dune field; these are the interdune, dune base, plinth and slipface communities. Their distribution along the dune elevation gradient appears to be limited mainly by differences in sand particle size, soil moisture and sand stability. It is hypothesized that the subtropical, coastal Namib desert has an inordinately heterogeneous, and probably unique, physical environment that contains several adaptative zones not found in temperate continental dune ecosystems. Under such conditions, there has existed a high potential for extensive adaptive radiations within the numerous lineages of the psammophilic ancestral biota.

Introduction

The Namib Desert sand dunes of southwestern Africa support an unusually diverse and endemic fauna (Koch, 1962). Thus far, the hypotheses proposed to explain this unusual diversity are the desert's great age (Koch, 1962) and the simultaneous occurrence of a cool coastal climate, a large dune surface area, and an arid-adapted ancestral fauna (Seely, 1978*a*). Although it is reasonable to assume that historical, climatic, geographic and phylogenetic factors have influenced the evolutionary development of this fauna, there have been no relevant data that suggest their causal relationships or relative importance.

During our ecological studies of the Namib dune biota, we have quantified various physical and biotic parameters of the dune environment, especially near Gobabeb, South West Africa/Namibia (23°34′S, 15°03′E). Our main purpose here is to describe and evaluate how and to what degree some of the dune's physical properties interact with the climate and with the biotic communities. Secondarily, we consider why the Namib environment may be unique among dune ecosystems, and what influences this may have had on speciation.

The physical environment

The Namib Desert of southwestern Africa covers approximately 270,000 km² (Koch, 1962) and, although it is only one-thirteenth the size of the Sahara Desert, it contains one of the world's major sand dune systems. This long and narrow dune field extends south from the

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vicinity of the Curoca River in Angola to the southern border of South West Africa/Namibia at the Orange River (Fig. 1). Its width varies from narrow strips of only 10 km to broader expanses of 140 km. North of the Swakop River to about 60 km north of the Huab River lies a gravel plain which divides the dunes into Northern and Southern subregions. Barnard (1973) estimates that the Southern dunes have an area of 34,000 km^2, and within it he recognizes three geomorphological provinces: the narrow coastal strip of transverse dunes; the linear dunes of the central area; and the multi-faceted dunes of the eastern section.

Dune morphology

Desert sand formations are variable and result mainly from underlying geomorphological features and regional wind patterns (Bagnold, 1954; Smith, 1968; Barnard, 1973; Besler, 1976*a*). The majority of the Southern Namib dune field is composed of long linear, or sief, dunes whose axes are oriented north–northwest to south–southeast. Linear dunes are separated by an interdune valley, or interdune, that varies in width from 0·1 to 3 km. Other dune formations that are scattered throughout the system are barchans, barchanoid ridges, and star dunes. Although their respective physiognomies are distinctive, all these dune formations share most of the topographic features described below. The nomenclatorial system for dune topography that we have adopted (Fig. 2) uses standardized geomorphological terms for sand formations (McKee, pers. comm.).

The dune base is the gently sloping lower portion of the leeward and windward slopes that overlies the basal substrate. Above the dune base is the plinth, which occurs on both the lee and windward slopes. The plinth and dune base are often lacking on barchan formations. The avalanche base (Fig. 2) is the juncture of the plinth with the steeply inclined (±30°)

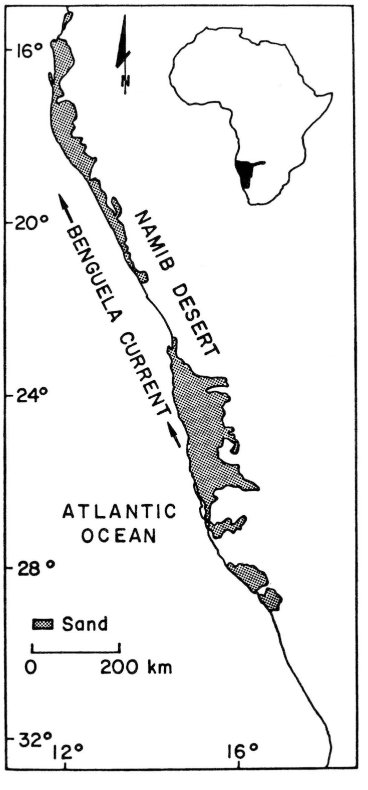

Figure 1. The coastal Namib Desert of southwestern Africa. The two major sand dune systems (shaded) are separated by approximately 130 km of gravel plains habitat.

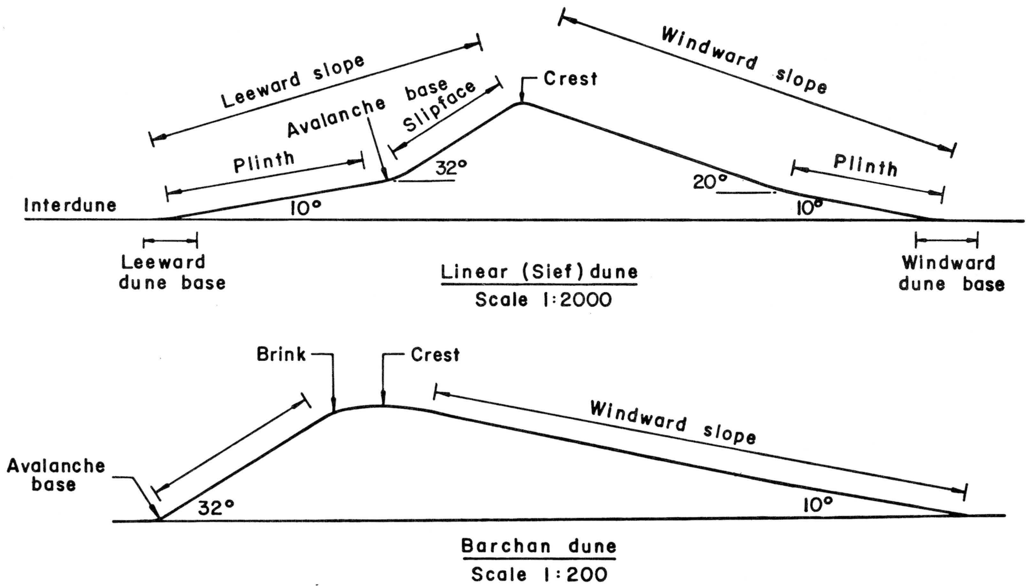

Figure 2. Topographically and ecologically distinct regions of a linear and a barchan dune.

slipface, and it is located only on the leeward slope. The dune crest is the highest point of a dune and is formed where the leeward and windward slopes meet; on barchan dunes the brink is the top of the slipface, and at times it may also be the highest point (crest).

Sand as a biotic medium

The parent material of sand is variable, but most sand is derived from quartz (Bagnold, 1954). Foth & Turk (1972) define sand as particles of 0·02–2·0 mm, but Bagnold (1954) limits the particle size to 0·01–1·0 mm. Dune sand is a soil that is extremely low in organic content, and because of this its physical properties are mainly determined by mineralogical and granulometric characteristics.

The pore size, or interstitial space, is a function of grain size; larger grains have larger pore spaces between them. The macropores are usually filled by gases, whereas micropores generally contain some water (Foth & Turk, 1972). The pore size and the pore volume of a soil directly affect such biologically important properties as aeration, moisture, temperature, insulation and light penetration. In most soils pore space comprises 40–60 per cent of the total volume, but the pore volume is less (30–35 per cent) in sandy soils (Foth & Turk, 1972). The bulk density (weight/volume dry soil) of sandy soil is greater (1·3–1·8) than finer textured soils (1·0–1·3), and this reduces the percent of the total soil volume that is occupied by the pore space (Foth & Turk, 1972). Soils with the greatest pore volumes have the lowest heat conduction rates (Ardo, 1957).

Sand has a large percentage of its total pore space composed of macropores, and this permits a faster exchange of water and gases, hence better aeration. Conversely, the low percentage of small pores in sandy soils gives them less water holding capacity. Air moves more freely through dry sand which has a greater volume of vacant pores; therefore, aeration is related to soil moisture (Foth & Turk, 1972). The specific heat of sand (quartz = 0·18) is less than water (1·0), so wet sand heats more slowly, but heat retention is longer. The heat conduction coefficient of dry sand (0·03) is much less than wet sand (0·13) (Ardo, 1957).

Several soil properties of dune sand from Gobabeb were determined (see Foth & Turk, 1972 for definitions and calculations). Sand from the slipface has a bulk density of 1·6 and the percent pore space is 35·4±0·8 per cent. Field capacity of one sample of fine slipface

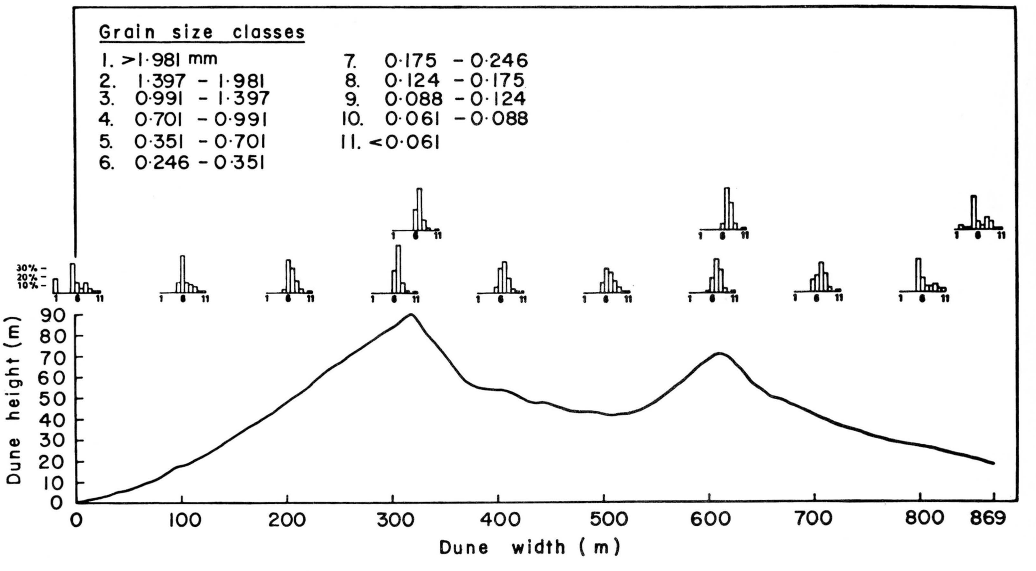

Figure 3. Frequency distributions of sand grain sizes across a double linear dune near Gobabeb. Histograms are above the site sampled.

sand was 6·4 per cent, while that of coarser plinth sand was only 2·5 per cent (Fölscher, pers comm.). Field capacity and the potential soil moisture, both of which affect several physical and biotic parameters (Table 2), can vary considerably depending on particle size, and changes in the modal particle size are generally predictable along a dune profile (Fig. 3).

Wind segregates sand grains according to their size (Bagnold, 1954). A topographic profile of the particle size distributions of a linear dune near Gobabeb is given in Fig. 3. The largest particles (>1·9 mm) occur at the leeward and windward dune bases where they may form 'megaripples' (Bagnold, 1954; Plate 1). Smaller grain sizes are more common as the windward slope is ascended, and in the intradune valley several smaller size-classes are co-dominant. Towards the lower half of the leeward slope larger particles are more frequent in the samples (Fig. 3). Besler (1976*b*) noted similar particle-size differences between crest and dune base sand at several Namib localities. Vegetation and other micro-relief anomalies may locally alter grain size distributions, but the overall trend is for coarser sands to occur towards the lower dune and finer sands upslope.

Sand colour is another biologically important characteristic, which is determined by the chemical and mineralogical composition of the parent rock. Solar reflectance and absorbance qualities change with surface coloration as do the amount of visible, infrared and shortwave radiation that is absorbed by a dune surface. These factors directly control the heating, cooling and water evaporation rates in the dunes. Namib coastal dunes are almost white, but to the east they become increasingly orange. Thus, the potential reflectance is greater in the coastal dunes than at inland localities.

Macroclimate

Past and present macroclimatic patterns that have caused desertic conditions along the coast of southwest Africa have been discussed by Wellington (1955), Logan (1960), van Zinderen Bakker (1975, 1976, 1978), Axelrod & Raven (1978), and Seely (1978*a*). Since 1962 meterological records have been collected from a first-order weather station at the Desert Ecological Research Unit (DERU) of the Namib Research Institute (23°34′S, 15°03′E). Five and ten year summaries of these data are provided by Schulze (1969) and Seely & Stuart (1976) respectively. The climatic trends discussed here for the northern part of the Southern dune field are based on these two references and unpublished DERU records.

The Namib is a cool, coastal desert with a mild warm-temperate to subtropical climate (Schulze & McGee, 1978, Fig. 4). Unlike continental temperate deserts there are no strong seasonal climatic changes. At Gobabeb the mean winter ambient temperature is 18·5 °C, and minimum values are seldom below 3 °C; summer air temperatures average 22·8 °C, and on very few days is the maximum above 40 °C (Fig. 5). Because of the frequent morning fogs and the high diurnal range of temperature and humidity, the inland region, including Gobabeb, has been termed an alternate fog desert (Besler, 1972). In contrast, the coastal fog desert has less diurnal temperature and humidity variation. The ecological climate diagram for Gobabeb (Fig. 4) illustrates several peculiarities of the Namib macroclimate.

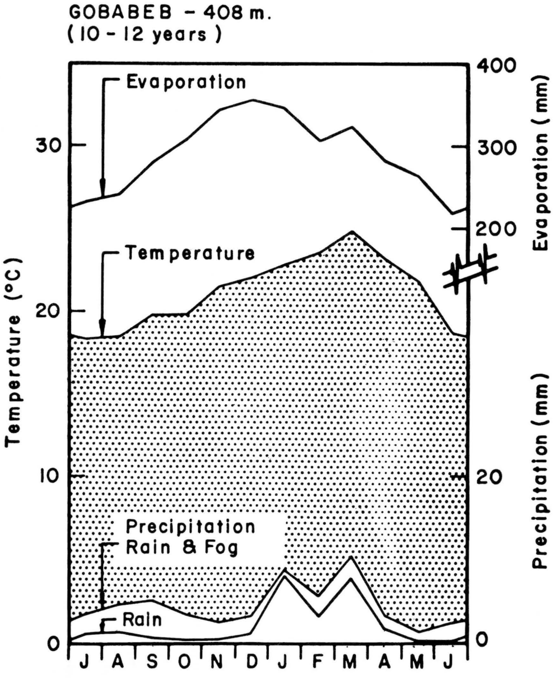

Figure 4. The ecological climate-diagram of Gobabeb (modified from Walter *et al.*, 1975). Months with maximum evaporation and maximum temperature do not coincide. Stippled area indicates the 'relatively droughty season'. Data from Seely & Stuart (1976) and unpublished DERU data.

The maximum evaporation rates (November–December) do not correspond with the period of highest temperatures (March), although a slight increase is evident at that time (Figs 4 and 5). This is due to the greater incidence of cloud cover from January to March. In maritime-dominated climates the monthly absolute minimum temperatures are generally fairly stable ($\pm$3–5°C), whereas monthly absolute maximum temperatures fluctuate widely (10–15°C) (Schulze, 1972). Although somewhat modified, this coastal influence on the temperature regime is apparent 56 km inland (Fig. 5).

Ambient relative humidity fluctuates from brief periods of 100%, under foggy conditions (Fig. 6(a)), to as low as 5 per cent or less during desiccating east winds (Fig. 6(b)). Rainfall is irregular in the Namib, but when it occurs, more than three-quarters (77 per cent) of the annual total falls in several events during the summer months of December to April (Fig. 7). At Gobabeb the average annual rainfall is 26·0 mm, but this has varied from as little as 2·2 to as much as 118 mm in 1976. The greatest rainfall ever recorded in the Namib, 140 mm, fell in 1934 (Watter, 1971). Precipitation of 15–20 mm in a period of several days initiates grass seed germination (Seely, 1978*b*) and the surface activity of several ephemeral species of insects (Holm, 1970). This amount of rainfall has occurred in three of the 11 years for which records (DERU) are available.

Advective fogs are common (±120 days per year) along the west coast of southern Africa (Nagel, 1962). Inland at Gobabeb, precipitating advective fogs are present an average of 36 days per year (Besler, 1972), and fog has been recorded in every month. Fog is an important source of moisture to the dune biota (Table 1), and in many years it contributes more to the total measurable precipitation than rainfall (Fig. 7). The coefficient of variation (CV) of the annual fog precipitation is three times less (38 per cent) than that of rainfall (127 per cent), and the occurrence of fog in a given month is about three times more likely (CV = 44 per cent) than rainfall (CV = 130 per cent). For the nine years that data are available, the measurable annual fog moisture varied from 11·0 to 37·8 mm ($\bar{x}$ = 26·7 mm). The importance of fog to the water economy of the dune biota appears to vary, but, in general, invertebrates seem to rely more on fog than do vertebrates. Among the invertebrates, the most elaborate fog-collection techniques are used by omnivorous coleoptera (Hamilton & Seely, 1976; Seely & Hamilton, 1976). One dune plant, *Trianthema hereroensis*, has also been shown to utilize fog water (Seely *et al.*, 1977).

Wind speed and direction have a strong influence on the physical and biotic environments of the Namib dune ecosystem (Table 2). Intraseasonal wind patterns at Gobabeb are varied, but an annual bi-directional regime is discernable. For four months of the year (May–August) strong (21 km/h) easterly to southeasterly winds predominate, but during the

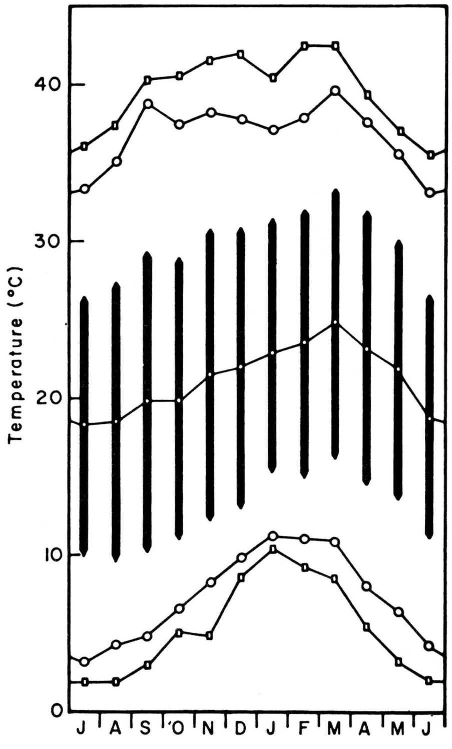

Figure 5. Ten-year summary (from Seely & Stuart, 1976) of the march of air temperature at Gobabeb. Square symbols are the absolute maximum and minimum, large circles are the ten year mean maximum and minimum, and small circles are the mean temperatures. Thick vertical lines connect the mean daily maximum and minimum (after Schulze, 1972). The mean diurnal temperature range (*c.* 17 °C) is much greater than the annual range of mean monthly temperatures (*c.* 4 °C).

remaining eight months weaker winds (13 km/h) from the north, northwest and southwest prevail (Schulze, 1969; Seely & Stuart, 1976). Species that forage on wind-blown detritus are usually more active during windy periods (Louw & Hamilton, 1972); desiccating east winds (Fig. 6(b)) do not normally reduce their surface activity.

Climatic gradients change rapidly across the desert's 100 km width to the extent that three macroclimates have been defined (Besler, 1972) within this short distance. Koch (1961, 1962) described a 'coastal' and 'inland' dune coleoptera fauna, and remarked that their

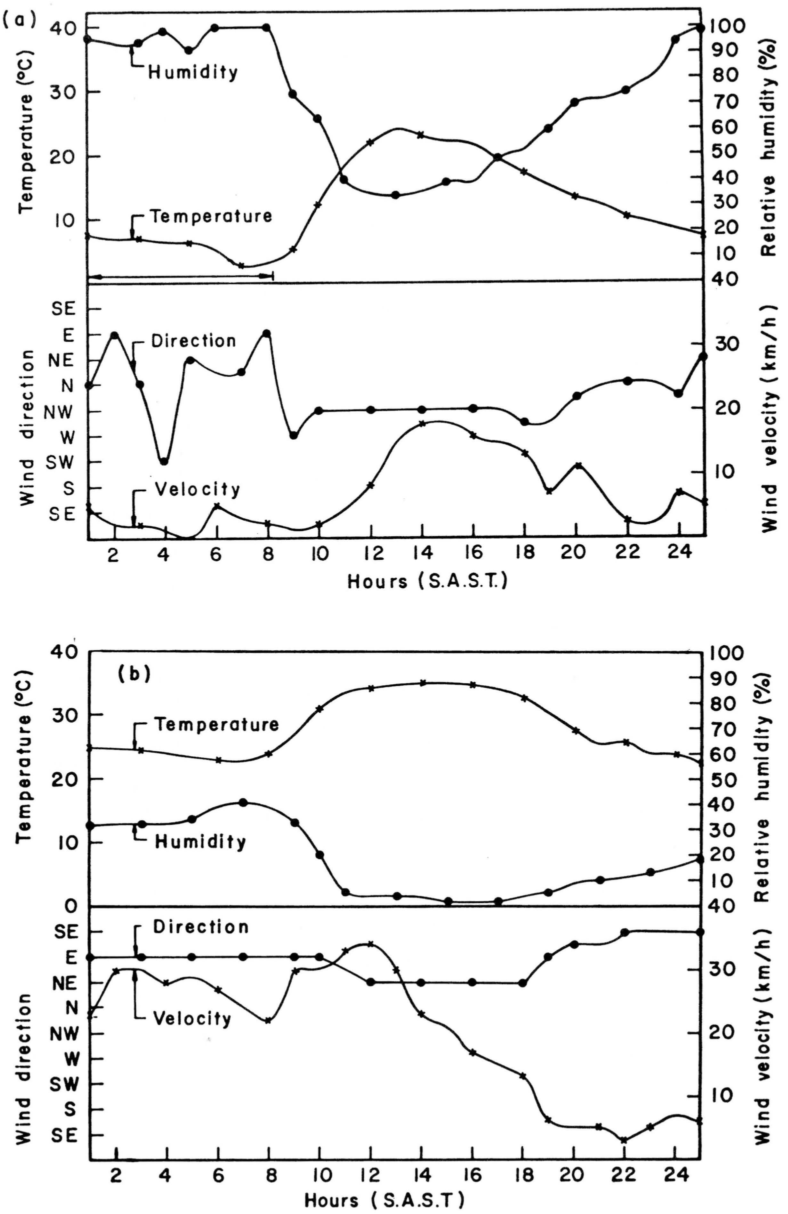

Figure 6. (a) Variation in ambient humidity, temperature, wind direction, and wind velocity during a typical foggy day (8 September 1971) at Gobabeb. (b) Same climatic parameters during a typical east wind day (27 April 1973); note the almost constant wind direction and low humidity. S.A.S.T. = South African Standard Time.

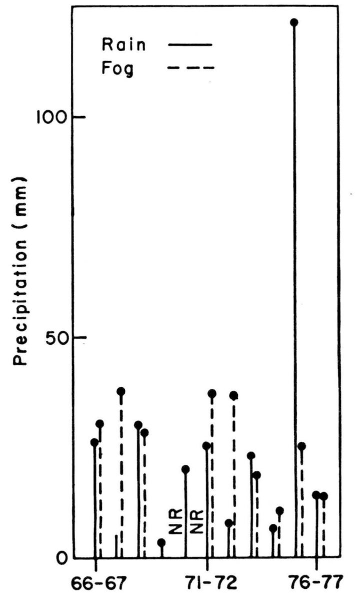

Figure 7. Extreme inter-year variation in total precipitation from fog and rain at Gobabeb (1966–77). No fog records (NR) available for 1969–71.

distributions roughly coincide with macroclimate shifts. Intuitively, such pronounced environmental gradients offer greater opportunity for ecological specialization, evolutionary divergence and increased species richness.

Microclimate

To dune plants and animals microclimate is the most relevant part of the climatic environment, and for the many smaller species more precise measurements than are presented here will be needed to properly understand their ecology. Useful microclimatological data for the Namib can also be found in papers by Hamilton (1971) and Holm & Edney (1973).

Winter and summer temperature profiles of various dune microenvironments are given in Fig. 8. Summer dune surface temperature may exceed 70 °C, but for most days it is less than 65 °C. Summer temperature cycles on clear and foggy days are compared in Fig. 8. The major effect of fog cover is that it retards the onset of dune surface heating, but subsurface temperatures are unaltered. Differences in maximum temperatures (Fig. 8) are the result of daily variation and, in this instance, not morning fog. Sudden changes in surface temperatures occur whenever winds begin (Fig. 8). At 10 cm summer subsurface temperature variation is approximately 20 °C, but at 20 cm thermal conditions are very stable (± 1 °C). In winter the maximum surface temperatures are generally 20 °C lower, while at 10 cm

Table 1. *Percent of total fog precipitated at five dune localities. Data summarized from 13 fogs*

Location on dune	Percent of total
Lower third, windward slope	13
Middle third, windward slope	22
Upper third, windward slope	32
Upper third, leeward slope	21
Middle third, leeward slope	10

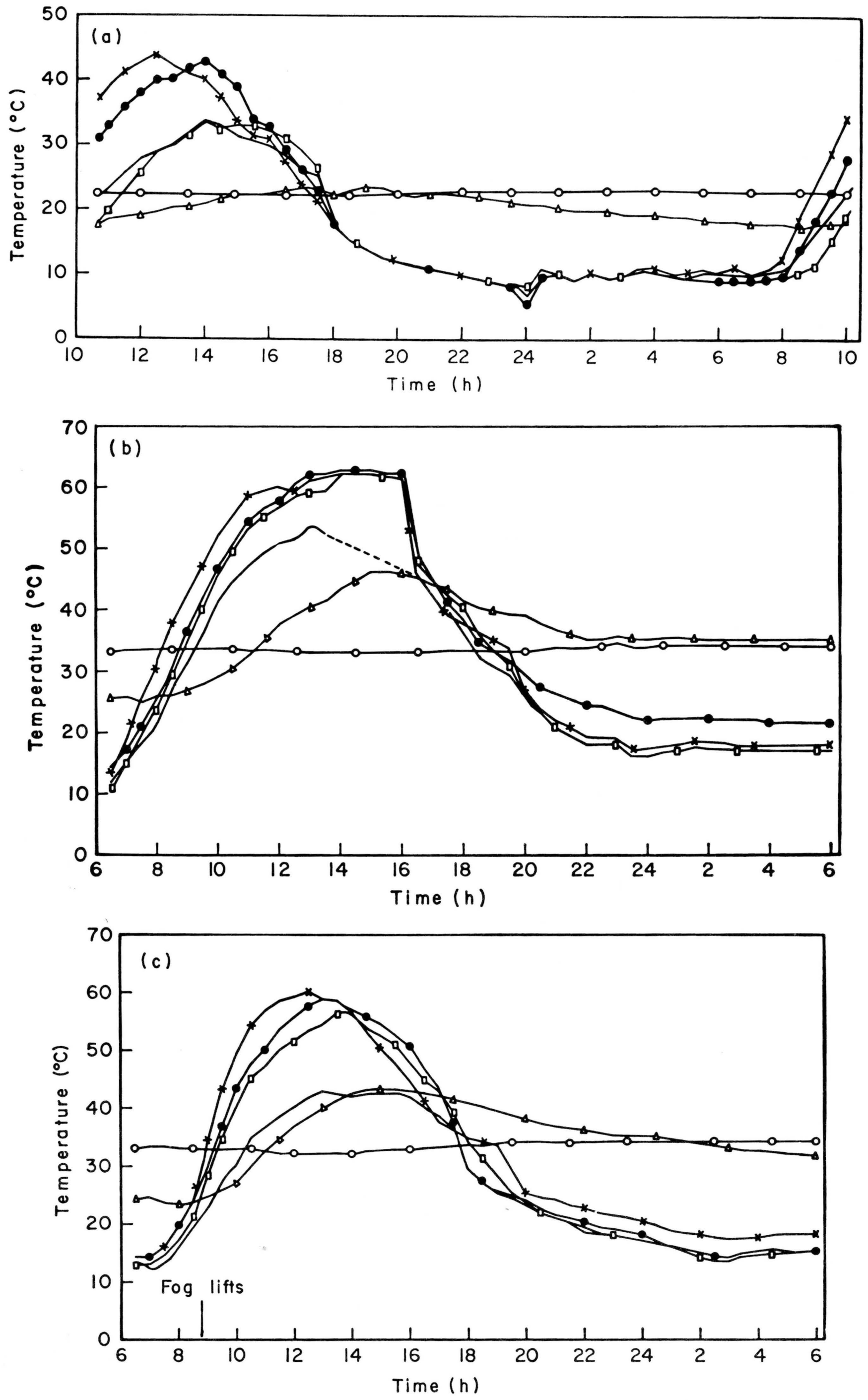

Figure 8. (a) Winter (30 June–1 July, 1977) dune temperature profile. Symbols for the six microhabitats are × = surface of a ENE-facing slipface; △ = slipface at 10 cm deep; ○ = slipface at 20 cm deep; □ = surface of windward slope, 8 m from crest; ○ = avalanche base; —— = surface of dune base. (b) Summer (19–20 December, 1977) dune temperature profile on a fogless day. (c) Summer (16–17 December, 1977) dune temperature profile on a foggy day. All symbols as in 8(a).

deep the average temperature (20·5 °C) is 13·3 °C less than in summer (33·8 °C). The mean summer and winter temperatures at 20 cm deep are 33·1 and 22·9 °C respectively. Sand, like other soils, has a considerable buffering effect on temperature extremes, but dune animals must bury to at least 20 cm to avoid lethal summer sand temperatures (Fig. 8(b)).

Because of the elevated slope angle ($\pm 30°$) and east to northeast orientation (except for periods when east winds reverse slipface direction), the sun strikes the dune slipface early in the morning and at a near-perpendicular angle. This produces a rapid surface heating rate in summer (0·17 °C min^{-1}) and in winter as well (0·11 °C min^{-1}). Summer surface temperatures are suitable for activity by most dune animals (20–45 °C) for approximately 1·8 h in the morning and 2·8 h in the afternoon (Fig. 9). The summer morning activity period can be extended slightly by movement to cooler dune regions such as the windward slope (Fig. 9).

In contrast to temperate continental climates there is considerably more nocturnal activity time available to ectothermic animals (Fig. 8), and numerous Namib dune species occupy this temporal niche (Appendix A).

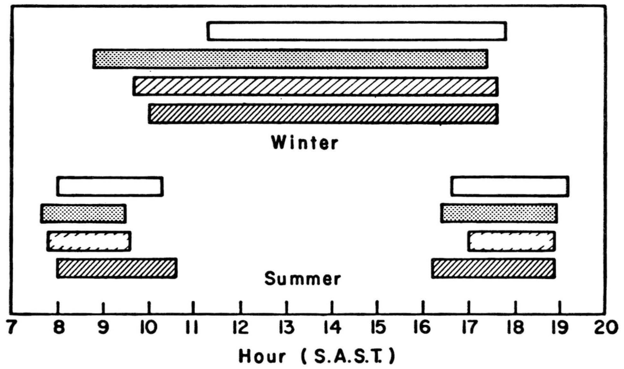

Figure 9. Seasonal variation in total time when diurnal dune surface temperatures on the windward slope (blank), slipface (stippled), avalanche base (wide hatching), and dune base (narrow hatching) are between 20–45 °C.

Slipface humidity at 10 cm and at the surface was measured using a Hygrodynamics portable hygrometer (model 15–3040). Figure 10 illustrates a representative 24 hour winter and summer cycle. Surface humidity varies widely from 100 per cent at night or early morning to a mid-day low of about 10 per cent, but humidity at 10 cm only fluctuates between 46 and 25 per cent. Surface humidity profiles have large daily variation depending on fog and wind events. Vapour pressure and dew point regimes can be derived from Figs 8 and 10. The subsurface environments where dune animals spend much of their lives remain at moderate humidities throughout the year, and animals can effectively reduce their evaporative water losses by remaining in this environment.

Rainfall and fog supply moisture to the dune sand, and of the two, water from rainfall is normally retained longest. Fog penetrates the top 1–2 cm, but this moisture usually evaporates within several hours. Rains usually penetrate deeper creating a wet horizon that may remain near the surface for several weeks. Capillary action and percolation gradually move the moisture downward where it is stored for long periods. This is why dunes that receive small amounts of precipitation support a greater-than-expected plant biomass (Zohary, 1973; 442). After rains of 3–14 mm the soil moisture in Gobabeb dunes varied from 2·2 to 8·0 per cent. Change in seasonal wind direction may remove the upper 20–50 cm of dry sand, uncovering patches of wet soil on the dune. The soil moisture of these areas is usually lower (0·9–2·6 per cent) than the field capacity. Mann *et al.* (1976) describe similar soil moisture conditions in dunes of western Rajasthan, India.

The amount of moisture that precipitates from a fog depends mainly on existing air temperature and vapour pressure gradients (Petterssen, 1969). Once on the surface, the moisture may be quickly evaporated by wind and sun before the fauna can utilize it. Due to the interaction of these variables, the amount of water that ultimately becomes available to the dune biota varies substantially with each fog. Moreover, certain topographic regions on the dune slope collect considerably more fog water than others (Table 1), and consequently not all dune communities benefit equally from a fog.

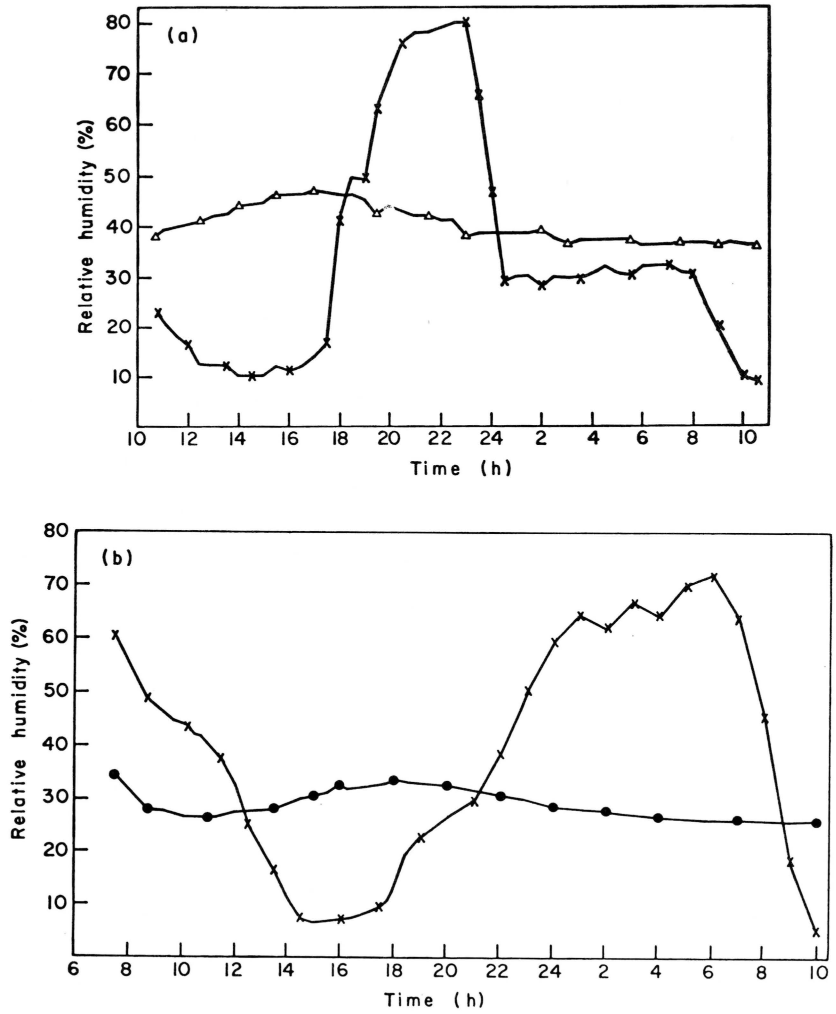

Figure 10. (a) Winter relative humidity cycle at the slipface surface (×), and at 10 cm deep (△). (b) Summer relative humidity cycle at the same sites. Humidity readings in 10(a) and 10(b) were made simultaneously to the temperatures in Figs 8(a) and 8(c) respectively.

Apparently light only penetrates the first few millimeters of sand. Black and white film (ASA 400) placed at 1 and 2 cm beneath sand gave no indication of light exposure after four hours. It would seem that light is effective as an environmental cue only when the organism is buried near the surface (<1 cm). Temperature, wind and humidity are several of the more obvious climatic parameters that dune animals appear to use to regulate their activities.

Dune morphology and aspect produce notable localized differences in microclimatology, Within a topographic region (e.g. plinth etc.) there is further climatic subdivision resulting in a complex mosaic of temperature, humidity, soil moisture and wind conditions. To an evolving biota, such a wide range of topographic variation and large and small-scale climatic diversity generates a high potential for ecological specialization and genetic divergence. Thus, it would seem that the heterogeneity of the physical environment of the Namib dune ecosystem has been a strong force in directing the evolutionary development of its diverse and endemic biota.

The biotic environment

Organic detritus

Wind-blown plant and animal detritus forms the trophic base for the fauna of the vegetationless slipface community. The major source of this detritus is the arid-adapted savannahs within and immediately surrounding the Namib dunes. After as little as 20 mm of rainfall these grassland communities can produce a considerable biomass (e.g. 10–20 kg ha^{-1}, Seely, 1978*b*). For some dune species detritus is the major source of nutrition, and since there is a wide seasonal variation in its abundance (Fig. 11), the potential importance of detritus as a limiting factor must be considered. Whether or not this same system of provenance, transport and storage of detritus occurs in other sand deserts is unknown.

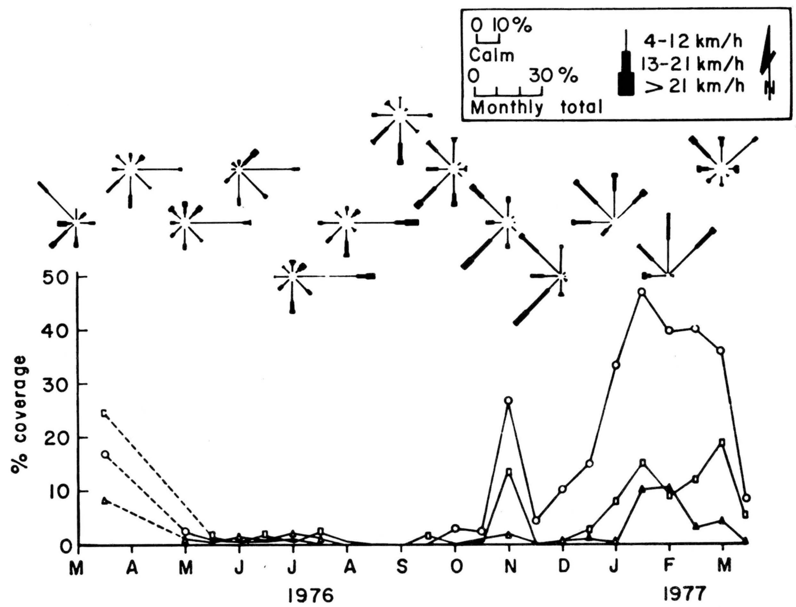

Figure 11. Percent coverage by wind-blown detritus on the slipfaces of three barchanoid ridges. Wind roses show monthly variations in wind strength, directions, and calms (centre diameter).

Detrital material in the Namib dune ecosystem is usually composed of plant leaves, stems, and seeds, but animal matter such as invertebrate exoskeletons, feathers and faeces occasionally account for as much as 10 per cent of a detrital sample. Brinck (1956) and Koch (1961, 1962) soon recognized the importance of organic detritus as a primary nutritional source for many dune species, but the amount and composition of this detritus, and the factors associated with its accumulation had not been quantified previously.

Wind distributes detritus through the dune system where it collects on the slipfaces of leeward slopes. The steep slipface ($\pm 30°$) creates a turbulence in the laminar flow of air as it passes over the windward slope, and a 'windshadow' develops on the lee side (Bagnold, 1954). As detritus and sand are carried over the crest and into the 'windshadow', they loose velocity, fall from the air stream, and become trapped on the relatively windless slipface. Sand accumulates at the crest until the surface layers shear away and cascade down the slipface, covering the organic materials in their path. Thus detritus is 'stored' in the dunes.

Later, when wind patterns change, the buried material is uncovered, redistributed, and eventually covered again.

Koch (1961, 1962) and others (Holm, 1970; Louw & Holm, 1972) have suggested that dune detritus originates in distant plant communities of the eastern plains and escarpment. Although some material probably enters the dunes from these grasslands, all the identifiable fragments in our samples were from local interdune or nearby plains species.

During 1976 we used the line-intercept method to measure the percent cover by wind-blown detritus on the slipface. In addition, we observed the movements of detritus during various wind storms, seasonal changes in coverage on three barchanoid ridges and shifts in the dominant wind direction and strength are illustrated in Fig. 11. When east winds begin (usually May) slipfaces are east-facing, and much of the detritus is blown across them and into the inter-dune. After several days of east winds, the slipfaces reverse and become west-facing. Then, some detritus collects on these newly established slipfaces, but the strong east winds continue to carry most of the material through the windshadow and off the dune. Buried detritus is uncovered and re-distributed by east winds, but the summer-grown vegetation is only beginning to dry and disintegrate at this time, so relatively little new material is added and stored. During east winds the surface coverage by detritus averaged less than 4 per cent. Throughout winter and into early spring coverage remains low, but from late spring to early autumn (November–March) it increases to 20–48 per cent. This increase coincides with the season of more gentle winds that come from the southwest, northwest, north and northeast (Fig. 11).

New detrital material is brought into the dune system after years of summer rain, when the biomass of the interdune and adjacent gravel plains grass species is highest. It appears that east winds serve primarily to transport and distribute autochthonous and allochthonous detritus to and within the dune ecosystem, but it is the weaker winds from the southwestern and northern quarters that deposit and trap most of it on the slipface where it can be utilized by the fauna. This period of detrital abundance coincides with the season of warmest temperatures and highest fog frequency, and we have observed this to be the time when many slipface species breed. Maps of detritus collection sites and analysis of line intercept data show that, on similarly oriented dunes, more detritus is trapped by certain dune morphologies, and on a given slipface detritus collects in specific microtopographic regions. Barchanoid formations collect more detritus than do straight linear dunes, and on each dune formation more material accumulates in the central concave part of the slipface and at the hooked, downwind end of the ridge. This creates a non-random distribution of the major nutritional resource in this dune community.

Brinck (1956) stated that sand at 'favourable' spots on the Northern Namib dunes contained 36·6 per cent organic material. To attain such a high organic percentage, samples must be drawn from surface detrital 'pads' which contain primarily macrodetrital fragments with proportionally little sand. During 1977, a year of high detritus production, the particulate (microdetrital) organic content of randomly sampled surface sand (0–5 cm) was highest at the avalanche base (2·0 per cent) and was less on the windward slope (0·8 per cent) and slipface (0·6 per cent). In a less productive period le Roux (1970) found lower values on the crest (0·02 per cent) and leeward slope (0·33 per cent). This food is utilized by the smallest dune invertebrates.

In the Negev desert, but not in the Namib dune desert, invertebrates have been observed eating moist detritus (Broza, 1979), but it is uncertain how much this moisture source contributes to their total water budget. Oven-dried plant material from the Namib gained 15–20 per cent weight (Tschinkel, 1973) when exposed to high humidities (90–100 per cent RH) for 10 hours, however, such extended periods of high humidities rarely exist in this dune habitat. Since the daily slipface humidity fluctuates so widely (Fig. 6), the amount of moisture derived from eating detritus would depend directly on the time of feeding.

The interaction of 10 physical and eight biotic parameters that have been discussed here are summarized in Table 2. Wind directly affects 12 of the 18 variables; fog and vegetation nine; soil temperature eight; and rain six. Dune morphology, which results directly from

The interdune community

Near Gobabeb the dunes rest on a reddish-grey limestone crust that contains large pebbles in the upper layers. Below about 20 cm, and to an unknown depth, is a fossil red sand (Scholz, 1972). Above this lies the shallow soil of the interdune community, which is usually covered by a coarse angular quartz lag gravel. The interdune (Plate 1) is almost level (0–6° slope) and its width varies from about 0·1–3·0 km.

After summer rains exceeding 15–20 mm, pure stands of the ephemeral grass, *Stipagrostis gonatostachys*, germinate and cover the interdune. Depending upon the amount and the temporal distribution of rainfall, the life cycle of this species can be completed in three to five weeks, or be extended for several months. The tallest plants (20–30 cm) grow at the juncture of the interdune and the dune base communities where more soil moisture is available for longer periods. After setting seed, some of these larger plants remained alive for more than one year. Perennial species such as *Stipagrostis ciliata*, *Tephrosia dregeana* and *Salsola tuberculata* occur near infrequent granite outcrops. During rainless years the interdune is almost devoid of gramineous vegetation. In regions where sand covers the interdune soil to a depth of at least 10 cm, plants of the dune base and lower plinth communities replace the interdune flora.

Small interdune animals burrow or use rocks and vegetation for shelter. Several beetles (e.g. *Eustolopus octoseriatus*, *Pachynotelus albonotatus*) depend on green plants for energy, and their life cycles are regulated by the occurrence of enough summer rain to produce new plant growth. Other interdune invertebrates feed on dry grass that collects at the plant bases. Unlike the ephemeral 'rain fauna' they are active throughout the year, or seasonally, but their population densities are much greater after rainfall years. Resident reptiles include four lizards and one snake. At least four taxa of common invertebrates and two vertebrates live only in the interdune (Appendix 1).

Several non-resident predators and grazers move into the interdune community when grass production and insect abundances are high. Predators include jackals, Ludwig's bustard and Ruppel's korhaan. Commonly seen herbivores and omnivores are the ostrich, Stark's lark, Gray's lark, grey-backed finch larks, pied and black crows, oryx and springbok. Cape hares and gerbils, which normally live in adjacent dune communities, move into the interdune when conditions are favourable.

The dune base community

The lower limit of this community corresponds to the extent that dune sand covers the interdune to a depth of about 10 cm. The upper boundary is formed by the inclined angle that marks the beginning of the plinth (Fig. 1, Plate 1). The soil is azonal and is composed of coarse sand (0·35–1·9 mm), which is often covered by a fine (2–8 mm) quartz lag deposit. Large (10–20 cm high) sand ridges or 'megaripples' form in localized regions where sand grains are largest (Plate 1). Although the average grain size of dune base sand is larger than in other dune areas (Fig. 3), the available soil moisture remains high, since gravitational water is periodically received from higher dune regions.

Vegetation cover is usually greatest in the dune base community. One plant, *Monsonia ignorata*, is almost totally restricted to this habitat. During dry periods the tubers of this geophyte persist in the stable sand, but above-surface growth and reproduction occur only after rains. Other plants characteristic of the dune base are grasses (*Asthenatherum glaucum*, *Eragrostis spinosa*), a lily (*Hexacyrtis dickiana*), and a leaf succulent (*Trianthema hereroensis*). Nara melon (*Acanthosicyos horrida*) is a locally abundant cucurbit that grows where ground water is near the surface. During dry periods dune base vegetation consists only of isolated individual plants of *T. hereroensis*.

Many animals construct shelters in the relatively stable sand of the dune base. Sand-swimming species, which do not build burrows, live in the loose sand at the base of plants. One tenebrionid beetle, *Cardiosis hamiltonuli*, lives only in the coarser sands of the dune base (Hamilton, 1971). Many other species of invertebrates and several reptiles and mammals are common in, but not limited to, this area (Appendix 1). In one dry period 35 invertebrate taxa were found associated with the dune succulent *T. hereroensis* (Seely *et al.*, 1977). Oryx preferentially graze *A. glaucum*, and sometimes they excavate and eat the moist tubers of *M. ignorata* or entire hummocks of *T. hereroensis* (pers. obs.). Several non-resident predators frequent this community (Appendix 1).

The plinth community

Compared with the dune base, plinth sands are finer (0·09–0·25 mm), generally less stable, and lower in soil moisture (pp. 185–6). Permanent burrows are possible in the finer plinth soils; non-burrowing species remain near the loose sand at the base of plants.

From the dune base, plant coverage decreases upslope, and is usually entirely absent in the upper third of the plinth. The most common plant, and the only one present during prolonged dry periods, is a dune-endemic grass, *Stipagrostis sabulicola.* Where the plinth slope is broader and less steep, this grass is often co-dominant with *T. hereroensis.* These two species often form large hummocks 1–2 m high, and they are shelter and activity centres for many invertebrates, the sidewinding adder, legless lizards, the golden mole, Cape hares, gerbils and Karoo larks. Detritus is trapped by these hummocks creating productive feeding sites for many omnivorous beetles and their larvae.

Plants growing in the dune base community may be locally abundant on the lower plinth. Barchanoid formations often lack a well-defined plinth, but a plinth community may be present at the contact zone between the lower windward slope and the interdune.

The slipface community

The dune slipface is clearly demarcated from the plinth by an abrupt change in slope angle at the avalanche base (Fig. 2). Besides the slipface and avalanche base, the crest and upper vegetationless portion of the windward slope constitute the slipface community. The slipface slopes are steep ($\pm 30°$) and very unstable with layers of surface sand periodically shearing away and cascading down to the avalanche base. This action, and the constant movement by wind, provide good aeration for the surface sands.

Normally, there are no living plants on the slipface; instead, the 'primary production' in this community is the wind-blown organic detritus, which accumulates on the surface. Occasionally, isolated plants of *S. sabulicola* and *T. hereroensis* are found on the slipface or at the avalanche base (Plate 2). This occurs when the slipface advances over existing plinth vegetation, or when there is germination at the avalanche base. In either case, the plants are eventually covered by sand, or, if the slipface is very small, they may stabilize it.

Except for the trap-door spiders (*Carparachne* and *Leuchorchestis*), who stabilize their burrows with a web, slipface animals cannot construct permanent burrows in the unstable sand. Instead, they rely on 'sand-swimming' to escape predators and unfavourable environmental conditions. Most of the species in this community range throughout its subdivisions (e.g. crest, windward slope, avalanche base), and less frequently they forage onto the plinth. Nevertheless, the majority of their activities are concentrated on the slipface and along the avalanche base. The percentage of nocturnal species is greater in this community (53 per cent) than in the others (Appendix 1).

Along the dune elevational gradient, plant community distribution appears mainly limited by differences in soil moisture and sand stability. In the flat interdune valley, soil is shallow and moisture storage is brief. Nevertheless, when rains are adequate, a remarkable biomass is produced by the arid-adapted ephemeral grassland. On the dune slopes, soil moisture and sand stability are generally greatest in the lower strata. Consequently, the perennial flora exists almost entirely in the dune base and plinth communities; plants cannot germinate nor become established on the dry and mobile slipfaces.

Summary

Although most dune ecosystems share certain physical characteristics such as structure, morphology and topography, their environments conditions are often very distinctive. Two

Plate 1. Megaripple region (foreground) of a dune base community. Grass (*Asthenatherum glaucum*) and a root-perennial (*Monsonia ignorata*) are the dominant plants. In the background is the interdune community with a pure stand of the ephemeral grass, *Stipagrostis gonatostachys*.

[*facing page* 198]

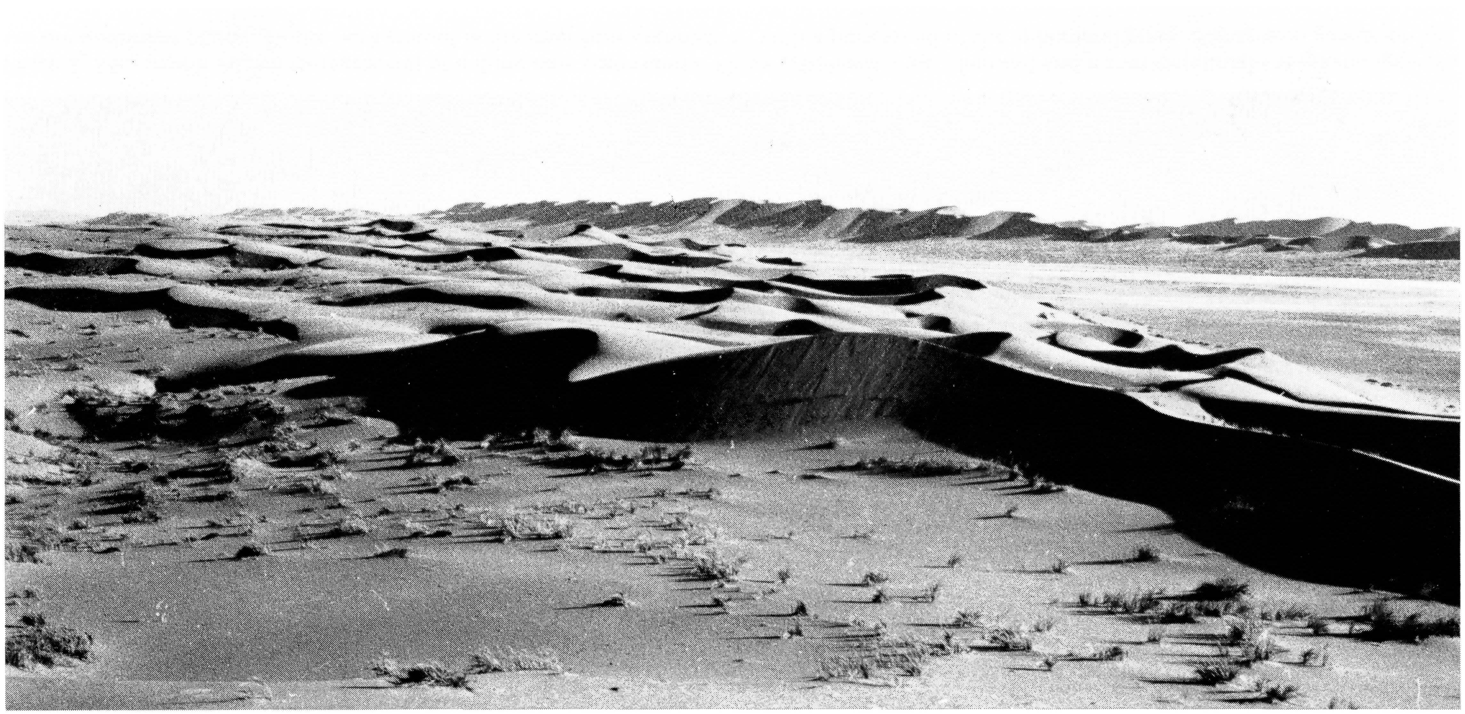

Plate 2. Linear dune (background), interdune, and a series of barchanoid ridges (foreground); the latter are advancing over a broad plinth and overrunning the vegetation (*Stipagrostis sabulicola*, and *Trianthema hereroensis*).

primary determinantes of dune macroclimate are the latitude of the dune system (tropical, subtropical, or temperate) and the continental location (i.e. coastal or interior).

The Namib dune desert of southwestern Africa has a mild but diverse subtropical climate that lacks any pronounced seasonal climatic change. In contrast to temperate or continental dunes, the mean monthly temperature varies annually by less than 5 °C, and freezing temperatures are rarely experienced. Climatic gradients change rapidly across the desert, and three macroclimates overlie the 100 km width. Dune orientation (aspect) and morphology subdivide micro- and macroclimate into a mosaic of distinctive microenvironments thereby increasing the ecological complexity.

Precipitating advective fog occurs approximately 120 days per year in the coastal dunes. and 56 km inland at Gobabeb the annual mean in 36 days. Fog is an important source of water for several Namib dune species, and, compared to rainfall, the occurrence of fog is about three times more predictable. Fog water frequently contributes the majority of the year's total precipitation in the dunes.

Wind-blown organic detritus is the major source of nutrition in several dune communities. Detrital abundance is related to seasonal wind patterns and the unpredictable primary productivity of the grassland communities. Detritus is periodically covered by sand and 'stored' beneath the surface. Then as seasonal wind directions change, it is uncovered and redistributed through the dune communities. Thus, some food is continually available to the primary consumers in this ecosystem, even during years when production and input of new organic material is very low.

Four dune communities are defined for this area: the interdune, dune base, plinth and slipface. Each community corresponds to a dune topographic unit, and each has a characteristic biota. The distribution of the plant species along the dune elevational gradient appears mainly limited by topography-specific differences in sand stability, particle size distribution and soil moisture.

Although similar data from other dune ecosystems are few, it appears that the Namib dunes have an uniquely heterogeneous physical environment. This diversity plus the relatively mild climates have produced several 'adaptative zones' for ectotherms that do not occur in temperate dunes. These, as well as other ecological characteristics, have been influential in shaping the evolution of the diverse Namib biota.

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References

Ardo, P. (1957). Studies in the marine shore dune ecosystem with special reference to the dipterous fauna. *Opuscula Entomologica, Supplementum* **14,** Lund: 225 pp.

Axelrod, D. I. & Raven, P. H. (1978). Late Cretaceous and Tertiary vegetation history of Africa. In Weger, M. J. A. (Ed.), *Biogeography and Ecology of Southern Africa*. Pp. 77–130. The Hague: Junk.

Bagnold, R. A. (1954). *The Physics of Blown Sand and Desert Dunes*. London: Methuen. 265 pp.

Barnard, W. S. (1973). Duinformasies in die Sentrale Namib. *Tegnikon*, December: 2–13.

Besler, H. (1972). Klimaverhältnisse und klimageomorphologische Zonierung der zentralen Namib (Südwestafrika). *Stuttgarter Geographische Studien*, **83**: 1–209.

Besler, H. (1976*a*). Untersuchungen in der Dunen-Namib (Südwestafrika). *Journal South West African Scientific Society*, **31**: 33–64.

Besler, H. (1976*b*). Wasserüberformte Dünen als Glied in der Landschaftsgenese der Namib. *Mitteilungen der Basler Africa Bibliographien*, **15**: 83–106.

Brinck, P. (1956). The food factor in animal desert life, in Wingstrand, K. G. (Ed.). *Bertil Hanstrom: Zoological Papers in honour of his 65th birthday, Nov. 20,* 1956. Pp. 120–137. Lund Zoological Institute: 312 pp.

Broza, M. (1979). Dew, fog and hygroscopic food as a source of water for desert arthropods. *Journal of Arid Environments*, **2**: 43–49.

Foth, H. D. & Turk, L. M. (1972). *Fundamentals of Soil Science*. New York: Wiley. 454 pp.

Hamilton III, W. J. (1971). Competition and thermoregulatory behavior of the Namib Desert tenebrionid beetle genus *Cardiosis*. *Ecology*, **52**: 810–822.

Hamilton III, W. J. & Seely, M. K. (1976). Fog basking by the Namib desert beetle, *Onymacris unguicularis*. *Nature*, **262**: 284–285.

Holm, E. (1970). The influence of climate on the activity patterns and abundance of xerophilous Namib Desert dune insects. M.Sc. Thesis. University of Pretoria, Pretoria, South Africa. 44 pp.

Holm, E. & Edney, E. B. (1973). Daily activity of Namib Desert arthropods in relation to climate. *Ecology*, **54**: 45–56.

Koch, C. (1961). Some aspects of abundant life in the vegetationless sand of the Namib Desert Dunes. *Journal South West African Scientific Society*, **15**: 8–34, 77–92.

Koch, C. (1962). The Tenebrionidae of southern Africa. XXXI. Comprehensive notes on the tenebrionid fauna of the Namib Desert. *Annals of the Transvaal Museum*, **24**: 61–106.

le Roux, G. J. (1970). The microbiology of sand-dune ecosystems in the Namib Desert. M.Sc. Thesis, University of Stellenbosch, Stellenbosch, South Africa. 97 pp.

Logan, R. F. (1960). *The Central Namib Desert, South West Africa*. Washington, D.C.: National Academy Science; National Research Council, Publication No. 758: 1–162.

Louw, G. N. & Hamilton III, W. J. (1972). Physiological and behavioural ecology of the ultrapsammophilous Namib Desert tenebrionid, *Lepidochora argentogrisea*. *Madoqua Series II*, **1**: 87–96.

Louw, G. N. & Holm, E. (1972). Physiological, morphological and behavioural adaptations of the ultrapsammophilous Namib Desert lizard, *Aporosaura anchietae* (Bocage). *Madoqua Series II*, 1: 67–85.

Mann, H. S., Lahiri, A. N. & Pareek, O. P. (1976). A study on the moisture availability and other conditions of unstabilised dunes in the context of present land use and the future prospects of diversification. *Annals of Arid Zones*, **15**: 270–284.

Nagel, J. F. (1962). Fog precipitation measurements on Africa's Southwest Coast, *Notos*, **1**: 51–60.

Petterssen, S. (1969). *Introduction to Meterology*. New York: McGraw-Hill. 333 pp.

Robinson, E. R. (1976). *Phytosociology of the Namib Desert Park*. M.Sc. Thesis, University of Natal, Pietermaritzburg, South Africa. 220 pp.

Scholz, H. (1972). The soils of the Central Namib Desert with special consideration of the soils in the vicinity of Gobabeb. *Madoqua Series II*, **1**: 33–51.

Schulze, B. R. (1969). The climate of Gobabeb. *Scientific Papers of the Namib Desert Research Station*, **38**: 5–12.

Schulze, B. R. (1972). South Africa. In Griffiths, J. F. (Ed.), *World Survey of Climatology, Vol. 10, Climates of Africa*. Pp. 501–586. Amsterdam: Elsevier Publ. Co. 604 pp.

Schulze, R. E. & McGee, O. S. (1978). Climatic indicies and classifications in relation to the biogeography of southern Africa. In Werger, M. J. A. (Ed.). *Biogeography and Ecology of Southern Africa*. Vol. **1**, pp. 19–52. The Hague: Dr. W. Junk Publ.

Seely, M. K. (1978*a*). The Namib Dune Desert: an unusual ecosystem. *Journal of Arid Environments*, **1**: 117–128.

Seely, M. K. (1978*b*). Grassland productivity: the desert end of the curve. *South African Journal of Science*, **74**: 295–297.

Seely, M. K., de Vos, M. P. & Louw, G. N. (1977). Fog imbibition, satellite fauna, and unusual leaf structure in a Namib Desert dune plant, *Trianthema hereroensis*. *South African Journal of Science*, **73**: 169–172.

Seely, M. K. & Hamilton, W. J. III. (1976). Fog catchment sand trenches constructed by tenebrionid beetles, *Lepidochora*, from the Namib Desert. *Science*, **193**: 484–486.

Seely, M. K. & Stuart, P. (1976). Namib climate: 2. The climate of Gobabeb; ten year summary 1962–1972. *Namib Bulletin*, **1**: 7–9.

Smith, H. T. U. (1968). Geologic and geomorphic aspects of deserts. In Brown, G. W. (Ed.), *Desert Biology*, vol. 1, pp. 51–100. New York: Academic Press. 635 pp.

Tschinkel, W. R. (1973). The sorption of water vapor by windborne plant debris in the Namib Desert. *Madoqua Series II*, **2**: 21–24.

van Zinderen-Bakker, E. M. (1975). The origin and paleoenvironment of the Namib Desert biome. *Journal of Biogeography*, **2**: 65–73.

van Zinderen-Bakker, E. M. (1976). The evolution of late Quaternary palaeoclimates of southern Africa. *Palaeoecology of Africa*, **9**: 160–202.

van Zinderen-Bakker, E. M. (1978). Quaternary vegetation changes in southern Africa. In Werger, M. J. A. (Ed.). *Biogeography and Ecology of Southern Africa*, vol. I, pp. 131–143. The Hague: Dr W. Junk.

Walter, H. (1971). *Ecology of Tropical and Subtropical Vegetation*. Edinburgh: Oliver and Boyd. 539 pp. and maps.

Walter, H., Harnickell, E. & Meuller-Dombois, D. (1975). Climate-diagram maps of the individual continents and the ecological climatic regions of the earth. *Supplement to the Vegetation Monographs*. Berlin: Springer-Verlag. 36 pp. and maps.

Wellington, J. H. 1955. *Southern Africa, a Geographical Study*. 2 vols. Cambridge: Cambridge University Press.

Zohary, M. (1973). *Geobotanical Foundations of the Middle East*. 2 vols. Stuttgart: Gustav Fischer Verlag. 739 pp.

Appendix 1

Ecological distribution and relative abundance of the common resident species in four dune communities in the Southern Namib dunes. Communities are the Interdune (ID), Dune Base (DB), Plinth (PL), Slipface (SF), and their lower (L) and upper (U) regions. Abundances are common (C), occasional (O), or rare (R); activity periods are nocturnal (N), diurnal (D), or crepuscular (C)

	Community						Activity
		L	U	L	U		
	ID	DB		PL		SF	
Plants							
Acanthosicyos horrida		O	R	R			
Asthenatherum glaucum		C	C	O			
Eragrostis spinosa		C	C	O			
Heliotropium ovalifolium	R						
Hexacyrtis dickiana		O					
Monsonia ignorata		C	O				
Salsola tuberculata	R						
Sesamum abbreviatum		O	O				
Stipagrostis ciliata	C						
S. gonatostachys	C	O					
S. lutescens		C					
S. sabulicola		O	O	C	C	R	
Tephrosia dregeana	R						
Trianthema hereroensis		C	C	O	O	R	
Mammals							
Canis mesomelas	O	O	O	O	O	O	D,C,N
Eremitalpa granti		O	C	C	C	O	N
Gerbillurus paeba	O	C	C	C	O	O	N
G. tytonus	O	C	C	C	O	O	N
Lepus capensis	O	C	C	C	R		D,N
Birds							
Cercomela tractrac	O						D
Certhilauda albescens		O	C	C			D

Appendix 1—*continued*

		Community					Activity
	ID	L DB	U DB	L PL	U PL	SF	
Reptiles							
Aporosaura anchietae					R	C	D
Bitis peringueyi		O	C	C	C	O	D,N
Chamaeleo namaquensis	O	O	O	O			D
Meroles cuneirostris	O	C	C	O			D
Palmatogecko rangei	O	C	C	C	C	C	N
Psammophis leightoni	O	C	C	O			D
P. notostictis	O	O	O				D
Ptenopus garrulus	C						N
P. kochi	C	O					N
Typhlosaurus braini		O	O	C	C		N,C
Invertebrates							
Order Scorpionida							
Opisthothalmus flavescens	C						N
Protophthalmus holmi		R	R	R	R		N
Order Aranea							
Caesetius deserticola					O	C	?
Carparachne alba				O	C	C	N
Leuchorchestris arenicola		C	C	C	O	O	N
Order Solpugida							
Metasolpuga picta	C						D
Solpuga lawrencei	R						D
Solpugista bicolor		C	C	C	C	O	D
Order Thysanura							
Ctenolepisma paulani		O	O	C	O		?
Ctenolepisma terebans		O	C	C	O		?
Hyperlepisma autralis	C						?
Morisma sp.			O	O	O	C	?
Order Orthoptera							
Acanthropus sp.		O	R	R			N
Comicus sp.		C	C	C	C	C	N
Crypsicercus cubicus	C	O	O				D
Order Hemiptera							
Pentatomidae		C	C	C	O		?
Order Coleoptera							
Archinamibia peezi			O	O	O		N
Brachyceras rotundatus	O	O	O	O			D
Carabidae		O	O	O	O		N
Cardiosis fairmairei		R	O	O	C	C	D,C
C. hamiltonuli		O	O				
Dactilocalcar caecus		C	C	O	O	O	C,N
Eustolopus octoseriatus	C	O	O	R	R	R	D
Lepidochora discoidalis				O	C	C	C,N
L. kahani				O	C	C	N
L. porti		C	C	O	O	R	N
Leptostethus (3 spp.)		C	C	C	O	O	D
Namibomodes serrimargo			C	C	O		N
Neopachysoma denticoli		C	C	C	O	R	D
N. rodriguesi		C	C	C			D
Onymacris laeviceps		R	O	C	C	C	D,C
O. plana	O	C	C	C	C	C	D

O. rugatipennis albotesselata	O	C	C	C	O		D
O. unguicularis			R	O	O	C	D
Pachynotelus albonatatus	C	O	O	O			D
P. comma	C	C	O				D
Psammogaster malani		O	C	C	C	O	C,N
Stenocara phylangium	C	C	O				D
Stips stahli		C	C	O			C,N
Vernayella delabati					O	C	N
V. epialtes					O	C	N
V. noctivaga					C	C	N
Zophosis moralesi	C	O	O	O	O	R	D
Z. orbicularis	C	O	O	R	R		D
Order Hymenoptera							
Camponotus detritus	O	C	C	C	O	R	D
Mutilidae sp.			O	O	O		D
Mutilidae sp.			R	R	R		D
Schizonyx aterrimus		C	C	C	C	O	D