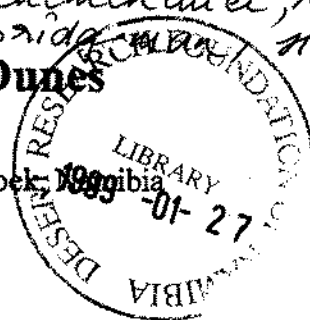


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The Ecology of Fog in Namib Desert Dunes

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Abstract: Mobile sand dunes occupy more than 70% of the length of the coastal Namib Desert, an area that receives less than 20 mm of rain per year. Fog occurs on 60-200 days per year making it a predictable source of water for desert organisms and the basis of functioning of the mobile dune ecosystem. Rain is essential for germination and establishment of two perennial plant species, one grass *Stipagrostis sabulicola* and one dwarf shrub *Trianthema hereroensis*, that use fog water for continued growth and reproduction. These two plant species support a vertebrate (lizards, golden mole) and invertebrate fauna (tenebrionid beetles, fish moths, termites, ants) that directly or indirectly use fog as their sole water source and wind blown plant detritus for much of their energy needs. As an arid and newly independent country with a long colonial history, the Namibian education system is looking for examples of functioning of arid ecosystems that are applicable if not unique to itself. The Namib fog ecosystem provides examples of marine-terrestrial interactions linked by fog, of the importance of water for living organisms, of the role of subsidies in energy-limited ecosystems, of the interactions between plants and animals, of adaptations to arid environments and it can be used to illustrate the concept of biodiversity and to draw attention to the potential effects of El Niño events and global climate change.

1. INTRODUCTION

The Namib Desert, lying along the south-western coast of Africa, supports an unusually diverse, endemic fauna. A variety of hypotheses have been advanced to explain this high diversity, particularly in the dune fauna. These include the apparent great age of the desert [Koch 1962], the diverse mosaic of substrates [Seely and Griffin 1986] and the presence of fog as a supplementary water source [Seely 1979].

The Namib Desert is thought to have been no moister than semi-arid for the last 80 million years. For the past 9 million years, the cold water Benguela upwelling system has been in place maintaining the hyper-arid climate [Ward *et al.* 1983]. Dune types in the Main Sand Sea vary from transverse dunes near the coast, to linear to multi-cyclic star dunes on the eastern edge of the dune field 130 km inland [Lancaster 1989]. All dune types are formed of similar components which provide specific habitats for surface dwelling fauna [Seely and Louw 1980].

The central and northern Namib experience summer rainfall while winter rainfall occurs in the south. Mean annual rainfall across the dune field ranges from 20 mm on the coast to above 80 mm on the eastern edge of the desert [Pietruszka and Seely 1985].

Fog is a more predictable and less variable moisture source than is rain [Pietruszka and Seely 1985]. The number of fog days ranges between 60 and 200 days per year and the amount of precipitation measured with a cylindrical screen ranges up to 180 mm per year [Seely and Henschel this volume]. The chemical composition of fog water indicates very low dissolved salt loads [Eckardt 1996].

2. USE OF FOG BY NAMIB DUNE PLANTS AND ANIMALS

2.1 Flora of the Sand Sea

More than ten species of vegetation germinate in the coastal portion of the Main Sand Sea dunes when rain falls, however, more than 50 mm are required for these plants to become established and reproduce [Seely and Louw 1980, Seely 1990]. Only two species of perennial vegetation, the 'dune grass' *Stipagrostis sabulicola* and the 'dune succulent' *Trianthema hereroensis*, are able to survive many years with little rain. Both are dependent on fog water for their longevity although both use different mechanisms for fog uptake and show different life history patterns [Louw and Seely 1980, Seely *et al.* 1977].

Stipagrostis sabulicola, a C4 grass, possesses an extensively developed lateral root system which can

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extend as far as 20 m from the main plant. The superficial location of the roots, mostly between 10-100 mm below the surface, facilitates uptake of fog moisture when surface sands reach field capacity [Louw and Seely 1980]. This regular source of moisture allows the dune grass to remain green throughout the year and live for several decades, flowering and producing seed annually. As a consequence, *S. sabulicola* represents a continuous source of plant detritus which supports many components of the dune fauna. *S. sabulicola* grows across the entire dune field.

Trianthema hereroensis is a C4 succulent in the family Aizoaceae which absorbs fog water directly through its leaves and green stems. The water is rapidly absorbed and translocated to the root system [Seely *et al.* 1977]. As a consequence, *T. hereroensis* remains green, flowers and produces seed throughout the year. Similar to *S. sabulicola*, *T. hererosensis* provides a continuous source of plant detritus and, in addition but unlike *S. sabulicola*, harbours a diverse and abundant satellite fauna. The dune succulent grows on the lower dune slopes restricted to the coastal fog zone.

Of particular note are the contrasting germination and establishment patterns on the dunes in relation to substrate stability and sand grain size influenced by fog availability [Seely 1990]. Where studied in the central Namib, germination of more than ten species of dune vegetation occurs over much of the dune surface. As the plants become established, however, very clear zonation develops, correlated with topographic position on the dune and mechanisms used by the plants to take-up moisture, in particular fog. The dune grass, *Stipagrostis sabulicola*, flourishes on the less stable, upper dune slopes where a mobile substrate is correlated with continual growth of new lateral roots. *Trianthema hereroensis* continues to grow on the more stable, coarse sand of the dune base.

Both species of dune plants that use fog as a supplementary moisture source grow continually throughout the year shedding leaves, dried flowers and seeds which accumulate at the slipface and around vegetation clumps on the dune surface [Robinson and Seely 1980]. On the surface, the plant detritus derived from these two fog dependent plant species provides an ever present source of energy for a variety of surface-feeding animals, although available biomass of detritus appears to be limiting populations during some periods [Crawford and Seely 1993]. When buried by mobile sand, another suite of animals takes advantage of this energy source [Crawford and Seely 1994].

2.2 Fauna of the Sand Sea

The fauna of the Namib Sand Sea has received particular attention since Koch [1962] described the diversity and unusual adaptations of the tenebrionid fauna of the Namib. Studies on behaviour, physiology, and population dynamics of the substrate-dependent vertebrate and invertebrate fauna have all referred to the influence of fog. A variety of species use fog directly as a primary source of free water (Table 1). These and other species, e.g. ants and termites [Curtis 1985], lizards [Robinson 1987], moles [Fielden *et al.* 1990] and other invertebrates rely on fog for water and energy, indirectly in the form of plant or animal materials that they consume.

Those sand dune species consuming free fog water either use their own bodies as condensation units, drink preformed droplets from the sand or plant surfaces or are able to absorb moisture from the unsaturated atmosphere. The table below summarises the current information concerning the variety of animals living in the Namib dunes taking advantage of fog water as a moisture source.

Animal species	A	B	C	R
Tenebrionid beetles				
<i>Lepidochora discoidalis</i>		x		1
<i>Onymacris unguicularis</i>	x			2
<i>Onymacris plana</i>		x		3
<i>Onymacris</i> spp. (larvae)			x	4
Termites				
<i>Psammotermes allocerus</i>		x		5
Fish moths				
<i>Ctenolepisma longicaudata</i>			x	6
Scorpions				
<i>Parabuthus villosus</i>	x			7
Spiders				
<i>Leucorchestris arenicola</i>		x		8
Reptiles				
<i>Bitis peringueyi</i>	x			9

Table 1 Namib fauna using fog water

(A = using own body as condensation unit; B= drinking preformed droplets or capillary water; C= absorbing moisture from unsaturated atmospheres; R= reference) (R1: Seely and Hamilton 1976; R2: Hamilton and Seely 1976; R3: Seely 1979; R4: Machin and O'Donnell 1991; R5: Grube and Rudolph 1995; R6: Edney 1971; R7: Polis and Seely 1990; R8: Henschel 1997; R9: Robinson and Hughes 1978.)

Physiological adaptations contributing to maintaining a positive water balance amongst a variety of the species using fog water, directly or indirectly, include low rates

water loss and tolerance of dehydration through efficient osmoregulation [Nicolson 1990].

The contradictory presence of a diuretic hormone in one desert dune tenebrionid remains unexplained [Nicolson and Hanrahan 1986]. Behavioural adaptations contributing to maintaining a positive water balance amongst species using fog water, directly or indirectly, include use of the sub-surface environment to avoid temperature extremes [Seely and Mitchell 1987] and tolerance of high temperatures while on the surface [Henwood 1995].

3. ROLE OF FOG IN THE NAMIB DUNE ECOSYSTEM

The Namib Desert dune ecosystem is an event driven system with rain as the primary water source but fog as a more predictable source. Use of fog water is one of a suite of abiotic factors, inter-related with winds, dune topography and sand consistency, that sustains this desert dune ecosystem [Seely 1983].

Fog has apparently contributed to the relatively high biodiversity of the Namib dunes by providing a continuous source of moisture in this rainfall driven system [Barnard 1998]. Plants and animals that would be present on an intermittent basis or not at all are able to continuously occupy the mobile dunes. In addition, fog supports not only the biota of the dunes but also plants and animals that occur elsewhere in the Namib, for example, the rich lichen fields on the gypsum plains and coastal hills as well as the winter rainfall system of the southern Namib Desert.

The occurrence of fog in the Namib dune ecosystem is closely related to the Benguela upwelling system of the southern Atlantic Ocean [Shannon *et al.* 1989]. The frequency and amount of fog onshore decreases with warmer waters near shore as accompany the equivalent of Pacific Ocean El Niño events, known as Benguela Niños. Although long term variability in the amount of upwelling and the condition of the Benguela system has been recorded [Shannon *et al.*, 1990, Bakun 1998] and variability of the upwelling system is expected to increase with Global Climate Change, the long term effects are as yet unknown. Although warming of the Benguela waters may result in more rainfall over the Namib, a decrease in the occurrence of fog would have a more decisive effect on the functioning of the sand dune ecosystem.

In the Namib dune ecosystem, fog can be considered as a water subsidy, that is, a source of moisture that allows the fauna to consume more of the available energy than

they would in its absence [Polis and Hurd 1995]. As a consequence, in some instances, food rather than water

becomes the limiting factor in this environment [Crawford and Seely 1993].

As an unusual, interesting and relatively well studied ecosystem in Namibia, a recently Independent, developing country, information concerning the Namib fog-based ecosystem has had many unexpected applications, not least of all its heuristic value. The Namib fog ecosystem represents:

- a well studied suite of adaptations by plants and animals to an extreme environment which can be examined in the light of prevailing aridity in Namibia;
- a good example of the meaning of biodiversity for life science classes;
- a well studied model of the potential effects of ENSO events and Global Climate Change that is not directly threatening to people's livelihoods in Namibia,
- an example of the effects of subsidies on a set of natural resources which can be compared to the drought subsidies of food and water for livestock which are a way of life in rural, arid Namibia.

As such, the fog-based ecosystem of the Namib dune desert assumes importance and is well known throughout Namibia despite its seeming lack of productivity for human use.

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