

Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



This article was published in an Elsevier journal. The attached copy is furnished to the author for non-commercial research and education use, including for instruction at the author's institution, sharing with colleagues and providing to institution administration.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>



Ecophysiology of atmospheric moisture in the Namib Desert

Joh R. Henschel^{a,*}, Mary K. Seely^{b,1}

^a Gobabeb Training and Research Centre, P.O.Box 953, Walvis Bay, Namibia

^b Desert Research Foundation of Namibia, P.O.Box 20232, Windhoek, Namibia

Abstract

Although the Namib Desert is classified as hyperarid, with rainfall extremely rare, there are several other sources of atmospheric moisture, namely, humidity, dew and fog, which make it possible for organisms to live there. Methods to use these sources include locating moist micro-climates, drinking from wet surfaces, consuming moist food, collecting water on the body, and absorbing water vapour. In describing these mechanisms from published sources, we highlight the work of Professor Gideon Louw, to whom we dedicate this paper. Louw's pioneering work on water relations and economy, which includes osmoregulation in desert plants and animals such as grass, beetles, and springbok, established a foundation that inspired numerous studies by colleagues and students. Ecophysiology provides many more lessons that have potential to be mimicked and applied in the occult collection of water in arid regions.

© 2007 Elsevier B.V. All rights reserved.

Keywords: Fog; Dew; Water vapour; Dampness; Absorption; Fog-collecting behaviour; Ecophysiological mechanisms

1. Introduction

All organisms require water (Louw, 1993). Water is the source of hydrogen for plants to reduce CO₂ and is also the source of oxygen that plants produce. As a good solvent of biochemicals and electrolytes it transports and facilitates chemical reactions, while acting as an important buffer system. Its thermal capacity and heat of vaporisation facilitate thermoregulation, while its poor compressibility enables hydraulic locomotion. The high surface tension of water facilitates drop formation and causes drops to run off hydrophobic bodies. All of these properties and more explain why life has evolved large-

ly around the unique properties of water (Louw, 1983, 1993).

Obtaining and retaining water is important for life in deserts. In hyperarid areas such as the Namib Desert, where rainfall is extremely rare and unpredictable, the occurrence of fog, dew and atmospheric moisture plays an important role in the water economy of many organisms. In this paper we review some of the knowledge relating to how Namib desert animals and plants obtain atmospheric moisture in this desert and comment on the (potential) application of this knowledge (Nelson, 2003).

In particular we present examples of Gideon Louw's observations and perspectives of his Namib work, and outline how his knowledge inspired others. Extensive contributions of this doyen of desert ecophysiology range from water, energy, and salt balance, to thermal biology, interpreted in terms of physiology, behaviour and ecology. He inspired a generation of students and

* Corresponding author. Fax: +264 64 694197.

E-mail addresses: joh.henschel@gobabeb.org (J.R. Henschel), mary.seely@drfn.org.na (M.K. Seely).

¹ Fax: +264 61 230172.

colleagues to elucidate these mechanisms and their consequences, and later reviewed some of these insights (Louw and Seely, 1982; Louw, 1990, 1993). With this paper we pay tribute to the late Professor Gideon Nel Louw who died on 22 March 2004.

Louw's first visit to the Gobabeb Training & Research Centre in the Namib Desert in 1966 followed the pioneering works by Walter (1936) and Koch (1961), who revealed that fog was important for life in the desert. Louw (1971, 1972) soon recognised that eco-physiological mechanisms were a key towards understanding the relationship between atmospheric moisture and desert organisms. He and subsequent workers described processes and patterns of Namib rain, fog, dew, and water vapour in relation to other micro-climatic factors such as temperature so as to understand the source of water, this rare commodity. They followed this with detailed observations or tests that revealed how organisms obtain water from these sources in damp micro-habitats, or by drinking from wet surfaces, consuming moistened food, using their bodies to collect water, or absorbing water vapour. In this paper we describe these observations and finally evaluate the significance of some of the insights.

2. Atmospheric moisture sources

2.1. Rain

The Namib Desert annually receives less than 50mm of rainfall and in its western half generally between 0 and 12mm. Although rain water is rarely available on the surface (Fig. 1), the effects of rain are extremely important for many life forms (Seely and Louw, 1980). After rainfall, plant biomass increases by an order of magnitude and then gradually declines over the course of the following dry years. Louw (1972) emphasised

that the ability to secure atmospheric moisture during the long periods between rainfalls is a key for survival of many Namib organisms.

2.2. Fog

Low stratocumulus clouds frequently enter the western part of the Namib Desert from the Atlantic Ocean (Lancaster et al., 1984) and deposit $0.1\text{--}1.01\text{ m}^{-2}\text{ day}^{-1}$ of fog water at particular sites (measured with vertical Standard Fog Collectors of 1 m^2) (Henschel et al., 1998; Fig. 2). This water is of low salt content (Eckardt and Schemenauer, 1998; Shanyengana et al., 2002) and its low osmolality of 14–38 m-osmole facilitates drinking (Louw, 1972). Fog water represents a relatively predictable, though temporary, source of free water for biota (Louw, 1971; Seely, 1979; Shanyengana, 2002).

2.3. Humidity

The near-ground atmosphere in the Namib is usually dry, e.g., at Gobabeb in 2001 relative humidity daily dropped below 50%, and on 90days it dropped below 20%. However, brief periods with high moisture do frequently occur, e.g., in 2001 at Gobabeb saturated air occurred on 189days, totalling 1015h over the year. The prevailing winds for most of the year are relatively cool SW–NW sea breezes that bring moist air into this area and reach saturation during at least some days of each month of the year (Lancaster et al., 1984; Fig. 3). Vapour pressure, caused by the difference between temperature above and below soil, facilitates the penetration of moisture into burrows during hot hours (Seely and Mitchell, 1987). Moisture conditions are therefore favourable for small animals in burrows by day when the above-surface air is hot, and the opposite is true by night (Louw, 1993). Burrowing nocturnal animals therefore experience the

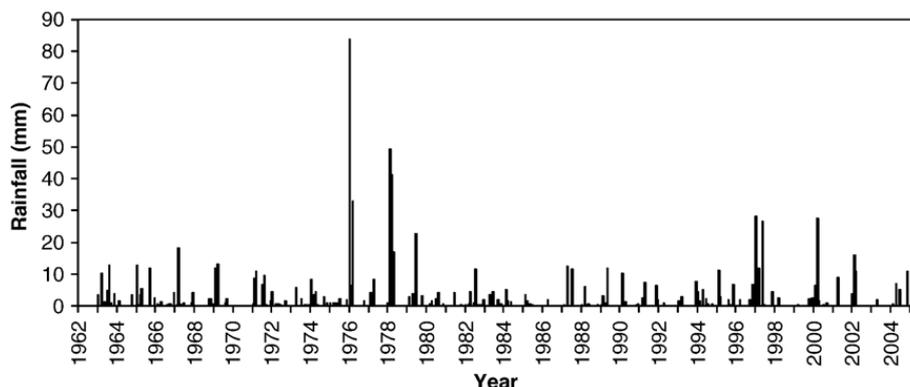


Fig. 1. Monthly rainfall recorded at Gobabeb between September 1962 and July 2005.

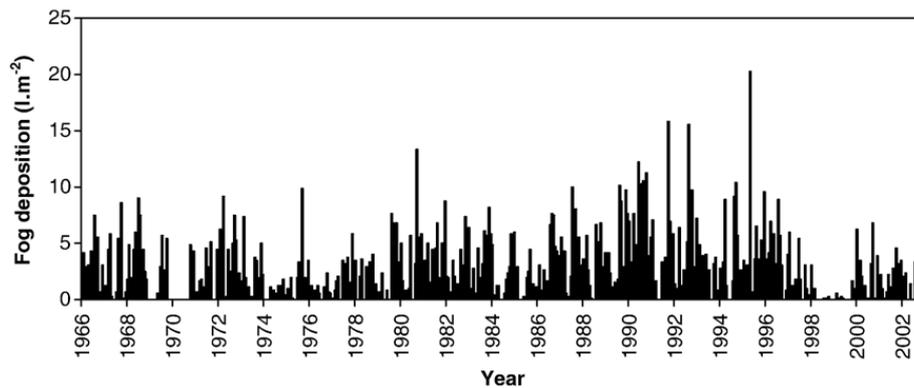


Fig. 2. Monthly fog deposition recorded at Gobabeb between January 1966 and December 2002.

desert as humid. Moist air reduces desiccation and is a potential source of water for organisms.

2.4. Dew

Dew is a phenomenon where water vapour condenses on a substrate and transforms into liquid water once the saturation pressure at the temperature of the substrate is lower than the saturation pressure at air temperature (Beysens, 1995). Dew has received little attention in the Namib, although it occurs very frequently during most of the year. For example, at Gobabeb during 2001, dew occurred during 53 nights (Fig. 3). By comparison, during the same year fog deposition (annual total 22.91 m^{-2}) occurred at Gobabeb during 67 nights, while rain (annual total = 10.3 mm) fell on 12 days (Fig. 3). This gives a total of 132 days (590 h) on which the soil surface was briefly wet. Thus even in this hyperarid place, free water in the form of rainfall, deposited fog or condensed dew occurs on surfaces about 40% of the days of a year. In this way atmospheric moisture can potentially become available to organisms in the form of free water. Namib dew should be studied in greater detail.

3. Atmospheric water acquisition

3.1. Damp micro-habitats

Moisture penetrates and lingers in sheltered micro-habitats under stones. Louw (1972) described how fog water deposition and dew condensation on stones trickles down the sides to below the stones where it supports the growth of *Fensteralgen* (Rumrich et al., 1989) and of a small community of invertebrates and micro-organisms. This micro-environment is even moist enough and has sufficient algal food to support snails *Xerocerastus minutus* (Hodgson et al., 1994).

3.2. Water uptake from wet surfaces

Louw and Holm (1971) noted the inability of southern slipface lizards, *Meroles anchietae*, to maintain condition solely on dry seeds alone, their normal diet. They recorded that these lizards drink water from wet surfaces and store it in an abdominal bladder, amounting to some 10% of body mass. Louw and Holm concluded that the occurrence of fog explains the survival of these lizards.

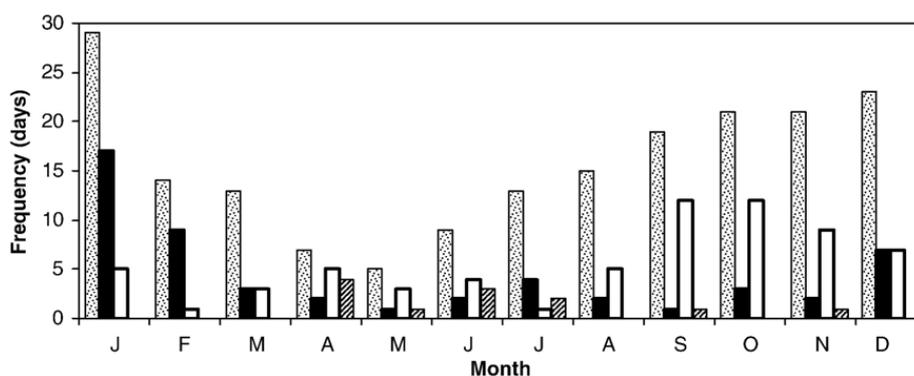


Fig. 3. Number of days per month on which saturated atmosphere (stippled bars; relative humidity >97%), dew (black; leaf wetness sensor), fog (clear; standard fog collector), and rain (shaded; electronic rain gauge, $\pm 0.1 \text{ mm}$) were recorded at Gobabeb during 2001.

Drinking of water drops from wet sand or vegetation has since been observed for many small animals (Seely et al., 1998) such as beetles (Seely, 1979), scorpions (Polis and Seely, 1990), and termites (Grube and Rudolph, 1995). The tenebrionids *Lepidochora* spp. enhance this mechanism by constructing 2–4 mm high ridges on dune surfaces perpendicular to the fog-bearing wind. This increases the water content of the surface sand and enables the beetles to collect fog water amounting to an average of 14% of their body mass (Seely and Hamilton, 1976). Incipient behaviour similar to this—drinking from bumps in the sand formed when beetles emerge from the sand—is performed by several *Zophosis* species (Seely, 1979). Although water imbibition has often been demonstrated (either gravimetrically or using tritiated water), the mechanism of drinking water from the sand is poorly understood (Nicolson, 1990). That this is special behaviour and not fortuitous uptake of water that animals happen to encounter is evidenced by these normally diurnal or crepuscular animals being active at times (late night) and temperatures (cool) that differ from their preferred foraging conditions (Louw and Hamilton, 1972; Holm and Edney, 1973; Seely, 1979).

Plants can also take up fog water from the sand surface. Using tritiated water, Louw and Seely (1980) demonstrated that a network of shallow, fine roots of the spiny dune grass *Stipagrostis sabulicola* absorbed water sprayed thinly on the dune surface adjacent to the plants (akin to fog), and transported this water up into the stem and leaves. The wetting of the sand surface around *S. sabulicola* is enhanced by fog drops collected in the grass canopy, from where they drip down.

3.3. Consumption of moistened food

The moisture content of dry grass increases corresponding to air humidity and can reach 27% at a relative humidity of 90% (Louw, 1972; Fig. 4). By feeding during cool, moist hours, particularly during fog or dew, animals as large as ostrich *Struthio camelus* (Louw, 1972) and springbok *Antidorcas marsupialis* (Louw and Seely, 1982; Nagy and Knight, 1994; Skinner and Louw, 1996) gain supplementary water that significantly increases their endurance in otherwise dry areas. This also appears to be the case for some rodents (*Petromyscus collinus*, *Aethomys namaquensis*, and *Petromys typicus*) living on Namib inselbergs which intercept fog (Withers et al., 1980). This is different for gerbils (*Gerbillurus* spp.), which balance their daily energy expenditure to daily water turnover rates so efficiently that water freed from oxidation of protein,

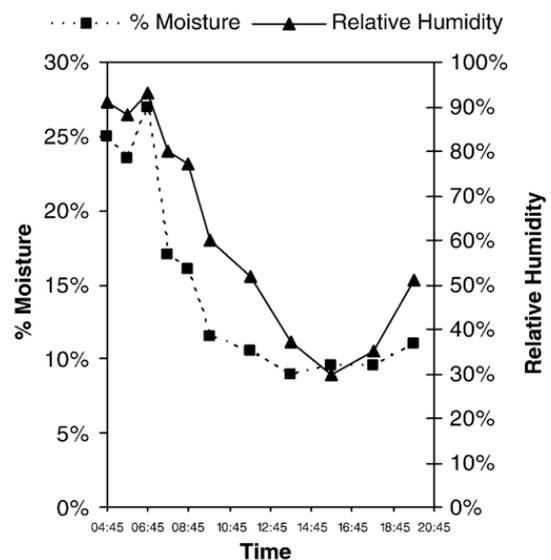


Fig. 4. Effect of relative humidity of air at various times on moisture content of the desert grass *Stipagrostis uniplumis* (after Louw, 1972).

fats and carbohydrates nearly satisfies their requirements. Gerbils can survive on air-dried seeds and have mechanism of reduced water loss (Buffenstein et al., 1985). However, they will consume moist food if available (Louw, 1972).

At the coast, fog water precipitates on the wings of Kelp flies. Southern slipface lizards *Meroles anchietae* living on the dunes adjacent to the ocean feed on these flies and thereby gain water. By feeding on the lizards, sidewinder adder *Bitis peringueyi* can, in turn, obtain this moisture (Louw, 1972).

3.4. Water collection on living surfaces

An even more specialised behaviour is fog-basking. Louw (1972) first described this behaviour for the sidewinder adder, *B. peringueyi*, which was later elaborated by Robinson and Hughes (1978). In fog, this snake flattens its body against the cool sand surface, thereby increasing the surface area exposed to water deposition. The snake licks water droplets off its body and periodically raises its head to swallow using gravity.

Fog-basking is also performed by the tenebrionid beetles *Onymacris bicolor* and *O. unguicularis* (Hamilton and Seely, 1976), diurnal species which climb up onto cool fog-swept dune crests at night and assume a head-down stance to allow fog to deposit onto their carapaces. Drops run down towards the mouth and the beetles drink, gaining an average of 12% of body weight. This behaviour is unique for these two species (Hamilton and Seely, 1976). The carapace surface characteristics of these *Onymacris* differs from that of other tenebrionid

species, as it has a continuous hydrophobic coating (droplet contact angle $>90^\circ$ compared to $<75^\circ$ for other species), a smooth texture and longitudinal ribbing (Shanyengana, 2002). Fog-basking has to date not been confirmed in nature for any other Namib beetle species with different carapace characteristics than these *Onymacris* spp. (Hamilton et al., 2003). Slobodchikoff and Wismann (1981) suggested that the large sub-elytral chamber of tenebrionids may permit the rapid expansion of the abdomen when quickly drinking large quantities of water.

It was demonstrated by the means of tritiated water that the dune succulent plant *Trianthema hereoensis* collects fog water on its leaves, imbibes this and transports some of it away from the leaves (Seely et al., 1977). Similarly, a dwarf shrub of the Central Namib gravel plains, *Arthroaerua leubnitziae* was shown, by means of dendrometers, to take up fog droplets through the leaves and translocate the water downwards to the root system (Loris, 2004). These plants lack hydathodes and the mechanism of water uptake by the leaves is unknown. Many species of *Crassula* from the southern Namib were shown to employ hydathodes to absorb water from wet leaf surfaces, and this absorbed water may subsequently stimulate carbon fixation rates, even in tissues distant from those wetted (Martin and von Willert, 2000).

Lichens directly absorb fog water that deposits on their surfaces (Schieferstein and Loris, 1992; Lalley, 2005), and the same applies to cyanobacteria and green algae (Lange et al., 1994). These poikilohydrous components of the soil crust are very sensitive to the exact state of precipitation or deposition of dew and fog on a micro scale. Spatial variation of this, for instance, accounts for zonation of lichens (Schieferstein and Loris, 1992; Lalley, 2005).

3.5. Absorption of water vapour

Lichens with green algae are able to take up water at air humidity above 96% (Lange et al., 1994). von Willert et al. (1992) discussed the possibility of water vapour uptake from saturated air in several succulents. In a process which they termed reverse transpiration, a negative water vapour gradient is established from outside towards the inside of the leaf when the leaf temperature is below ambient air temperature and the stomata are open. In this way these plants can gain 17–49% in weight on humid nights.

Passive absorption of water vapour is very common in arthropods (Hadley, 1994; Chown and Nicolson, 2004). Reduced water loss and increased absorption

would explain why relative humidity is one of the factors next to temperature and wind that influences the activity pattern of surface-active arthropods in the Namib (Holm and Edney, 1973), and differences of these factors between microhabitat may affect arthropod distribution (Holm and Scholtz, 1980).

Some arthropods can actively take up atmospheric water vapour from unsaturated air (Edney, 1977; Hadley, 1994). This is only possible above a critical equilibrium activity (CEA), the threshold at which water efflux equals vapour influx (Hadley, 1994). Active absorption requires energy, especially remarkable in deserts where energy from food is limited (Louw and Seely, 1982). Nevertheless, the amount of energy required for this is relatively little, only a few percent compared to the basal metabolic rate (Edney, 1977; Hadley, 1994). Active absorption of vapour is limited to animals of very small size, well below 1 g (Machin et al., 1982).

Absorption of water from air at a relative humidity far below saturation, as low as 47.5%, has been recorded for Namib thysanurans *Ctenolepisma* spp. (Heeg, 1967; Edney, 1971). Thysanurans apply rectal ion pumps to create osmotic gradients that draw water vapour from unsaturated air. Different mechanisms have also been found in other arthropods (Edney, 1977; Hadley, 1994), e.g. the oral water vapour uptake system of the Californian desert cockroach *Arenivaga* (Edney, 1966), but these other mechanisms have not been studied in the Namib.

In field experiments, Rössl (2000) found that when atmospheric moisture was prevented from reaching larvae of eight Namib tenebrionid species, all larvae

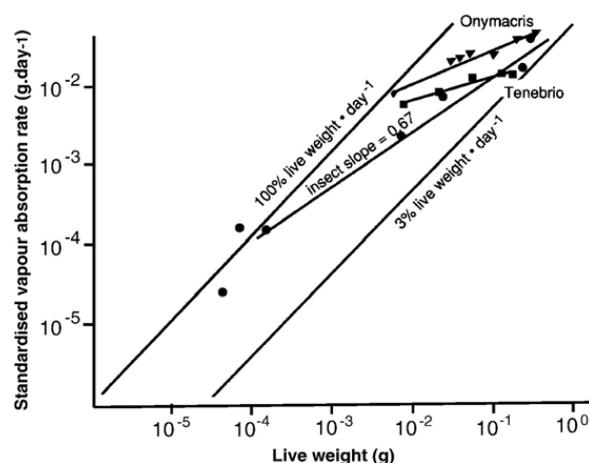


Fig. 5. Standardised vapour absorption rates (g day^{-1}) for insects of different size, showing insects in general (circles), *Tenebrio* (squares) and *Onymacris* (triangles) (after Machin et al., 1982).

of three species died and the others developed more slowly, indicating dependence on atmospheric moisture. The mechanism was studied in larvae of the Namib tenebrionids *Onymacris marginipennis* and *O. plana*. The larvae come to the surface at night and use a specialised, complex structure of their rectal cavity to absorb water vapour (Machin et al., 1982). Extreme concentrations of KCl in the Malpighian tubules generates osmotic pressure that go up to an extraordinary 9 Osmol, compared to 0.6 Osmol in the haemolymph. The standardised vapour absorption rate by *Onymacris* is the highest recorded for any similar-sized insects and can in small individuals nearly reach 100% of the larval live weight per day, which has otherwise only been recorded in animals that are 1% the size of these beetles (Machin et al., 1982; Hadley, 1994) (Fig. 5). Louw (1990) highlighted that this is indeed 'special' to desert animals.

Similar to the absorption of atmospheric moisture is the resorption of water from saturated exhaled air by the ostrich in its respiratory tract, which conserves 25% of its daily water turnover (Withers et al., 1981).

4. Conclusions

Even in a hyperarid environment there are a number of ways for organisms to obtain atmospheric water, namely a) location in moist micro-environments, b) drinking from wet surfaces during dew or fog, c) consumption of moistened food, d) collecting fog water on the body, and e) absorbing water vapour. Both (d) and (e) involve some special adaptations, notably fog-basking, and formation of high osmotic pressure. These mechanisms do not scale up easily.

Applications for fog-and dew-water collection have already started to make use of some of these biological principles. For instance some of the above mechanisms apply to the Zibold well that collects water under stones (mechanism a; Nikolayev et al., 1996), the atmospheric well of Knapen makes use of vapour pressure gradients (a), and there are also counterparts in nature for dew condensers (b; Beysens et al., 2004), the Krumsvik water pyramid (c), and standard fog collectors (d; Schemenauer and Cereceda, 1994). However, the active mechanisms to absorb water vapour are, indeed, special and unique to small desert animals and have not been mimicked. Further detailed studies of ecophysiological mechanisms could perhaps help to improve existing applications. Challenging would be finding cost-effective methods to use osmotic pressure or extremely fine hydrophilic structures coupled with pumps to obtain water from unsaturated air.

Louw's legacy leaves us with the portrayal of life as a hydrological process and a broad message concerning its conservation, not least for its invaluable lessons on survival and the potential for its application for collection of water in deserts.

Acknowledgements

Climatic data were recorded by the Desert Research Foundation of Namibia at Gobabeb. The Ministry of Environment and Tourism gave permission to conduct research in the Namib. We thank Yvette Evans, Bill Hamilton, Elsita Kiekebusch, John Pallett and two anonymous referees for comments.

References

- Beysens, D., 1995. The formation of dew. *Atmos. Res.* 39, 215–237.
- Beysens, D., Muselli, M., Milimouk, I., Ohayon, C., Berkowicz, S., Soyeux, E., Mileta, M., Ortega, P., 2004. Passive radiative condensers to extract water from air. *Bull. Croat. Met. Soc.* 39, 59–69.
- Buffenstein, R., Campbell, W.E., Jarvis, J.U.M., 1985. Identification of crystalline allantoin in the urine of African Cricetidae (Rodentia) and its role in their water economy. *J. Comp. Physiol. B* 155, 493–499.
- Chown, S.L., Nicolson, S.W., 2004. *Insect Physiological Ecology*. Oxford University Press, Oxford.
- Eckardt, F.D., Schemenauer, R.S., 1998. Fog water chemistry in the Namib Desert, Namibia. *Atmos. Environ.* 32, 2595–2599.
- Edney, E.B., 1966. Absorption of water vapour from unsaturated air by *Arenivaga* (Polyphagidae, Dictyoptera). *Comp. Biochem. Phys.* 19, 387–408.
- Edney, E.B., 1971. Some aspects of water balance in tenebrionid beetles and a thysanuran from the Namib Desert of southern Africa. *Physiol. Zool.* 44, 61–76.
- Edney, E.B., 1977. *Water Balance in Land Arthropods*. Springer-Verlag, Berlin.
- Grube, S., Rudolph, D., 1995. Termites in arid environments: the water balance of *Psammotermes allocerus* Silvestri. *Mitt. Dtsch. Ges. Allg. Angew. Entomol.* 10, 665–668.
- Hadley, N.F., 1994. *Water Relations of Terrestrial Arthropods*. Academic Press, New York.
- Hamilton III, W.J., Seely, M.K., 1976. Fog basking by the Namib Desert beetle, *Onymacris unguicularis*. *Nature*, 262, 284–285.
- Hamilton III, W.J., Henschel, J.R., Seely, M.K., 2003. Fog collection by Namib Desert beetles. *S. Afr. J. Sci.* 99, 181.
- Heeg, J., 1967. Studies on Thysanura: 1. The water economy of *Machioides delanyii* (Wygodzinsky) and *Ctenolepisma longicaudata* (Escherich). *Zool. Afr* 3, 21–41.
- Henschel, J.R., Mtuleni, V., Gruntkowski, N., Seely, M.K., Shanyengana, E.S., 1998. Namfog: Namibian application of fog-collecting systems, Phase 1: evaluation of fog-water harvesting. Desert Research Foundation of Namibia, Occasional paper no.8. Windhoek, Namibia.
- Hodgson, A.N., Hänel, C., Loveridge, A.J., 1994. The reproductive cycle of the pulmonate snail *Xerocerastus minutus* from the Namib Desert. *J. Molluscan Stud.* 60, 355–358.
- Holm, E., Edney, E.B., 1973. Daily activity of Namib Desert arthropods in relation to climate. *Ecology* 54, 45–56.

- Holm, E., Scholtz, C.H., 1980. Structure and pattern of the Namib Desert dune ecosystem at Gobabeb. *Madoqua* 12, 3–39.
- Koch, C., 1961. Some aspects of abundant life in the vegetationless sand of the Namib Desert dunes. *J. SWA Sci. Soc.* 15, 9–34.
- Lalley, J.S., 2005. Lichen-dominated soil crusts in the hyper-arid Namib Desert: anthropogenic impacts and conservation implications. Ph.D. Thesis, University of Oxford, Oxford, UK.
- Lancaster, J., Lancaster, N., Seely, M.K., 1984. Climate of the central Namib Desert. *Madoqua* 14, 5–61.
- Lange, O.L., Meyer, A., Zellner, H., Heber, U., 1994. Photosynthesis and water relations of lichen soil crusts: field measurements in the coastal fog zone of the Namib Desert. *Funct. Ecol.* 8, 253–264.
- Loris, K., 2004. Nebel als Wasserressource für den Strauch *Arthroa leubnitziae*. In: Walter, H., Breckle, S.-W. (Eds.), *Ökologie der Erde: Spezielle Ökologie der tropischen und subtropischen Zonen*, vol. 2. Spektrum-Verlag, pp. 485–489.
- Louw, G.N., 1971. Water economy of certain Namib Desert animals. *S. Afr. J. Sci.* 67, 119–123.
- Louw, G.N., 1972. The role of advective fog in the water economy of certain Namib Desert animals. *Symp. Zool. Soc. Lond.* 31, 297–314.
- Louw, G.N., 1983. Water and desert survival. *Rössing Mag.* 1983, 16–20.
- Louw, G.N., 1990. Physiological studies on the Namib fauna: a brief critique. In: Seely, M.K. (Ed.), *Namib ecology: 25 years of Namib research*. Transvaal Museum Monograph, vol. 7. Pretoria, pp. 203–207.
- Louw, G.N., 1993. *Physiological Animal Ecology*. Longman Scientific and Technical, Essex.
- Louw, G.N., Hamilton, W.J.I., 1972. Physiological and behavioural ecology of the ultrapsammophilous Namib Desert tenebrionid, *Lepidochora argentogrisea*. *Madoqua*, Ser. II 1, 87–95.
- Louw, G.N., Holm, E., 1971. Physiological, morphological and behavioural adaptations of the ultrapsammophilous Namib Desert lizard *Aporosaura anchietae* (Bocage). *Madoqua*, Ser. II 1, 67–85.
- Louw, G.N., Seely, M.K., 1980. Exploitation of fog water by a perennial Namib dune grass *Stipagrostis sabulicola*. *S. Afr. J. Sci.* 76, 38–39.
- Louw, G.N., Seely, M.K., 1982. *Ecology of Desert Organisms*. Longman, London and New York.
- Machin, J., O'Donnell, M.J., Coutchie, P.A., 1982. Mechanisms of water vapor absorption in insects. *J. Exp. Zool.* 222, 309–320.
- Martin, C.E., von Willert, D.J., 2000. Leaf epidermal hydathodes and the ecophysiological consequences for foliar water uptake in the species of *Crassula* from the Namib Desert in Southern Africa. *Plant Biol.* 2, 229–242.
- Nagy, K.A., Knight, M.H., 1994. Energy, water, and food use by springbok antelope (*Antidorcas marsupialis*) in the Kalahari Desert. *J. Mammal.* 75, 860–872.
- Nelson, R.A., 2003. Air wells—methods for recovery of atmospheric humidity. www.rexresearch.com/airwells/airwells.htm.
- Nikolayev, V.S., Beysens, D., Gioda, A., Milimouk, I., Katiushin, E., Morel, J.-P., 1996. Water recovery from dew. *J. Hydrol.* 182, 19–35.
- Nicolson, S.W., 1990. Water relations of the Namib tenebrionid beetles. In: Seely, M.K. (Ed.), *Namib ecology: 25 years of Namib research*. Transvaal Museum Monograph, vol. 7. Pretoria, pp. 173–178.
- Polis, G.A., Seely, M.K., 1990. Imbibition of precipitated fog by Namib Desert scorpions. *J. Arachnol.* 18, 362–363.
- Robinson, M.D., Hughes, D.A., 1978. Observations on the natural history of Peringuey's adder, *Bitis peringueyi* (Boulenger) (Reptilia: Viperidae). *Ann. Transv. Mus.* 31, 190–196.
- Rössl, R., 2000. Reproduktionsbiologie, Entwicklungsbiologie und Ökologie von sympatrischen Tenebrionidae (Coleoptera: Insecta) des Kuiseb bei Gobabeb in der Namib Wüste, Namibia. Ph.D. Thesis, Rheinische Friedrich-Wilhelms-Universität, Bonn, Germany.
- Rumrich, R., Rumrich, M., Lange-Bertalot, H., 1989. Diatomeen als "Fensteralgen" in der Namib-Wüste und anderen ariden Gebieten von SWA/Namibia. *Dinteria* 20, 23–29.
- Schemenauer, R.S., Cereceda, P., 1994. A proposed standard fog collector for use in high-elevation regions. *J. Appl. Meteorol.* 33, 1313–1322.
- Schieferstein, B., Loris, K., 1992. Ecological investigations on lichen fields of the Central Namib. *Vegetatio* 98, 113–128.
- Seely, M.K., 1979. Irregular fog as a water source for desert dune beetles. *Oecologia* 42, 213–227.
- Seely, M.K., Hamilton, W.J., 1976. Fog catchment sand trenches constructed by tenebrionid beetles, *Lepidochora*, from the Namib Desert. *Science* 193, 484–486.
- Seely, M.K., Louw, G.N., 1980. First approximation of the effects of rainfall on the ecology and energetics of a Namib Desert dune ecosystem. *J. Arid Environ.* 3, 25–54.
- Seely, M.K., Mitchell, D., 1987. Is the subsurface environment of the Namib Desert dunes a thermal haven for chthonic beetles. *S. Afr. J. Zool.* 22, 57–61.
- Seely, M.K., de Vos, M.P., Louw, G.N., 1977. Fog imbibition, satellite fauna and unusual leaf structure in a Namib Desert dune plant, *Trianthema hereroensis*. *S. Afr. J. Sci.* 73, 169–172.
- Seely, M.K., Henschel, J.R., Robertson, M., 1998. The ecology of fog in Namib sand dunes. In: Schemenauer, R.S., Bridgman, H. (Eds.), *Proceedings: 1st International Conference on Fog and Fog Collection*. Vancouver, Canada, pp. 183–186.
- Shanyengana, E.S., 2002. Groundwater chemistry and supplementary sources of freshwater in arid environments: groundwater salinisation, solar desalination and fog collection. Ph.D. Thesis, Department of Chemistry, University of Stellenbosch, South Africa.
- Shanyengana, E.S., Henschel, J.R., Seely, M.K., Sanderson, R.D., 2002. Exploring fog as a supplementary water source in Namibia. *J. Atmos. Res.* 64, 251–259.
- Skinner, J.D., Louw, G.N., 1996. The Springbok-*Antidorcas marsupialis* (Zimmerman, 1780). Transvaal Museum Monograph, vol. 10. Pretoria.
- Slobodchikoff, C.N., Wismann, K., 1981. A function of the sub-elytral chamber of tenebrionid beetles. *J. Exp. Biol.* 90, 109–114.
- von Willert, D.J., Eller, B.M., Werger, M.J.A., Brinckmann, E., Ihlenfeldt, H.D., 1992. *Life strategies of succulents in deserts*. Cambridge Studies in Ecology. Cambridge University Press, Cambridge.
- Walter, H., 1936. *Die ökologischen Verhältnisse in der Namib-Nebelwüste (Südwestafrika)*. Gebrüder Borntraeger, Leipzig.
- Withers, P.C., Louw, G.N., Henschel, J.R., 1980. Energetics and water relations in Namib Desert rodents. *S. Afr. J. Zool.* 15, 131–137.
- Withers, P.C., Siegfried, W.R., Louw, G.N., 1981. Desert ostrich exhales unsaturated air. *S. Afr. J. Sci.* 77, 569–570.