Exploitation of Fog Water by a Perennial Namib Dune Grass, *Stipagrotis sabulicola*

Fog is an important abiotic factor in the ecology of the coastal Namib Desert[1] and has been implicated in the physiology of the plants and animals living there.[2,3] Although only lichens can be considered true fog plants,[4] the use of fog, at least as a supplementary source of water, has been demonstrated in two vascular plant species.[5,6]

In the extensive Namib dune sea there are only two species of perennial plants that are able to survive for many years with little or no rain (<20 mm/yr). These are *Trianthema hereroensis,* a leaf succulent, and the coarse dune grass *Stipagrostis sabulicola* (Pilger) De Winter. We have previously established that *T. hereroensis* is capable of imbibing large amounts of tritiated water rapidly when this material is sprayed on the leaves.[6] In view of the restricted distribution of *T. hereroensis* within the fog zone of the Namib Desert and its prolonged survival under extremely arid conditions, we concluded that fog imbibition through the leaves was an essential process in the water balance of this species.[6] Consequently, we consider it equally important to examine the possibility that the only other species capable of prolonged survival under the same conditions (*S. sabulicola*) could also utilize precipitated fog water.

A study of the morphology of the roots and leaves of *S. sabulicola,* however, revealed that its leaves and root system are entirely different from that of *T. hereroensis.* In contrast to *T. hereroensis, S. sabulicola* has a poorly developed vertical root system which seldom penetrates the sand to depths greater than 70 cm. The leaves of *S. sabulicola* are also tightly rolled into spikes and present a much smaller surface area for fog collection than *T. hereroensis.* On the other hand, unlike *T. hereroensis, S. sabulicola* possesses an extensively developed lateral root system which can extend as far as 20 m from the main plant. These laterally running adventitious roots may serve to help anchor the plant in the shifting sandy substrate, but their superficial location suggested to us that they may also be involved in the absorption of precipitated fog water on the surface of the dune. Their actual depth beneath the surface of the sand varies mostly between 1 – 10 cm, depending upon wind action on the unstable sandy substrate (Fig. 1). At any given time, however, a substantial portion of this complex lateral root system either lies within the first centimetre beneath the surface of the sand or is entirely exposed to the atmosphere. In these situations the roots and root hairs are frequently exposed to surface temperatures in excess of 50°C and on occasion to temperatures as high as 70°C. The first centimetre beneath the surface of the dune sand also frequently reaches field capacity as a result of condensation of fog water on the surface, while the sand beneath the first centimetre remains dry. This led us to test the hypothesis that these superficial lateral roots are capable of absorbing condensed fog water in contrast to the already demonstrated leaf absorption by *T. hereroensis.*

Fig. 1. A portion of the extensive lateral root system of *S.* [illegible]

Two large individuals of *S. sabulicola,* growing on the typical dune slope habitat, were selected for treatment. The amount of water required per unit surface area to bring only the top centimetre of dune sand to field capacity had been determined previously on a separate but similar test site. The same volume of tritiated water was then applied on a segment of sand, measuring 14 m^2, adjacent to each plant, making certain that no water came into direct contact with the leaves, roots and stems of the main plant. We wished, however, to test the hypothesis that the shallow dampening of the sand, simulating fog precipitation, would bring at least some tritiated water into contact with a portion of the lateral root system. The water was applied to the sand surface at 04h00 when low temperatures prevailed (15.5°C and 92% R.H.), typical of the time and conditions under which fog naturally occurs. Twenty-six hours later five samples of approximately 25 g of plant material were removed from each plant at each of the following positions: lateral roots, vertical roots beneath main plant, and the green stems plus leaves, thereby providing 30 samples in total. The samples were sealed in air-tight glass vials and refrigerated for later analysis.

Table 1. Tritium concentration (cpm per gram wet tissue) for the three *S. sabulicola* tissues sampled from two plants at one day and seven weeks after application to surrounding sand. (Means derived from a total of 10 subsamples, five from each plant.)

Samples and sampling time	Mean concentration	± S.E.	Mean concentration after drying	± S.E.
One day				
Stem and leaves	2130	±490	~0	–
Main vertical roots	9530	±1 770	~0	–
Lateral roots	19490	±4 325	~0	–
Seven weeks				
Stem and leaves	86	±60	~0	–
Main vertical roots	5860	±1 745	3 060	±910
Lateral roots	8720	±1 295	6 270	±920

Seven weeks after the water treatment the same plants were sampled in an identical manner for the second time. The plant material was weighed in the laboratory before being homogenised in a measured volume of double-distilled water. The homogenate was then centrifuged in a refrigerated high speed centrifuge and an aliquot of the supernatant was treated with hydrogen peroxide before mixing with scintillation fluid (Insta-Gel) and counting. In addition to the above analyses, the 7-week sample was also dried at 100°C until a constant mass was obtained before mixing with double-distilled water and counting. This procedure was used to determine what fraction of the original free water in the one-day sample had been incorporated into soluble photosynthates in the plants.

The results in Table 1 show that in both of the treated plants, the labelled water was absorbed from the top centimetre of the dune sand by the lateral roots and translocated within 26 h to the main vertical roots and the leaves. We therefore concluded that the very extensive and superficial root system of this species enables it to exploit the irregular condensing fogs which are a feature of the Namib dune ecosystem. Moreover, this facility is probably of key importance in ensuring the survival of this species for many years with little or no rain. This conclusion is supported by the distribution of this species, as it is endemic to the southern Namib dune sea and the Atlantic fog belt. Unlike *T. hereroensis,* which is restricted to the western half of the dune sea, its range extends to the eastern periphery of the dunes where rain replaces fog as the major source rain in this area as efficiently as condensed fog water. Nevertheless, it is significant that in this area the plants are distributed mostly near the crests of the dunes where fog precipitation is maximal and where the extensive lateral root system also allows the plants to survive on a highly unstable sandy substrate.

The data in Table 1 also show that after seven weeks almost no radioactivity was present in the green leaves and stems. The main vertical roots and lateral roots, however, contained large amounts of tritiated material. Because a larger percentage of this radioactivity still remained after drying, prior to homogenizing in water, it can be concluded that most of the tritium in these organs had been incorporated into photosynthates. Nevertheless, some tritiated water was still present in these organs and this fact, together with the high counts obtained for photosynthates, suggest that these C_4 plants[7] make very efficient use of water, thereby allowing them to survive on the occasional exploitation of precipitated fog water.

In spite of the importance of fog water in the survival of this species, it should be noted that at least 20 mm of rain is required for its successful germination (Seely, unpublished results).

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Nitrogen Excretion by the Juvenile Prawn *Penaeus indicus* Milne Edwards at Various Temperatures

Most aquatic crustacea are ammoniotelic,[1] since ammonia is energetically the most efficient means of excreting nitrogen. Although ammonia is toxic, its toxicity is never realised in nature owing to its dilution in the surrounding water. In crowded conditions, such as those that might exist when tropical prawns are grown for research or aquacultural purposes, ammonia levels rapidly increase and have a detrimental effect on the growth of the animals. Wickins[2] calculated a 'maximum acceptable level' of total nitrogen as ammonia ($NH_4^+ - N$) which reduced the growth of several prawn species by 1 to 2% of that of controls to be 1.9 mg $NH_4^+ - N$ per litre at 33‰, 28°C and pH 8.0. In order to avoid exceeding this level because of excessive crowding or inadequate biological filtration, a knowledge of the rate of nitrogen excretion by penaeid prawns is required. In this paper quantitative data on the nitrogen excretion of ***Penaeus indicus*** Milne Edwards are given.

Total nitrogen and nitrogen as ammonia excreted by *P. indicus* over a 24 hour period (12:12 light, dark photoperiod) were determined at 28°C ($n = 29$); 24°C ($n = 21$), 20°C ($n = 22$) and 16°C ($n = 21$). Total nitrogen was measured by the micro-Kjeldahl method, while total ammonia determinations were carried out by titration with 0.01 N HCl after steam distillation in a Parnas-Wagner apparatus.[3]

The prawns ranged from 1 to 12 g fresh mass and were netted from the Amatikulu and Fish River estuaries, South Africa. All animals used were at the intermoult stage, since Needham[4] found premoult fluctuations in the nitrogen excretion of *Carcinides maenas* (Pennant). Prawns were held in large volume (600 litre) sub-gravel filtration systems in the laboratory for a minimum period of 2 weeks before use. During this time they were fed *ad libitum* with a formulated pellet containing approximately 54% protein. Prawns were acclimated for 48 hours to the various temperatures before determination of their excretion rates. In addition, only prawns with full guts were investigated since no feeding was allowed during the experiments.

Depending on the size of prawns used, experiments were carried out in glass containers with between 300 and 1 000 ml of filtered (Whatman GF/C) sea water. In order to remove any volatile bases which might have been present, air was passed through concentrated H_2SO_4 before being used to aerate the sea water containing the prawns.[5] After the experiments, aliquots of sea water in which the prawns were held were once again filtered through Whatman GF/C filter paper to remove faecal material, and then analysed for total nitrogen and nitrogen as ammonia.

Although an experimental period of 24 hours has been used to determine excretion rates of a variety of aquatic animals,[6-8] it has been subject to criticism. Webb and Johannes[9] found that after 24 hours, bacterial populations in their 75 ml containers had reached a density of 0.5×10^6 ml^{-1} and removed 30% of the dissolved amino acids. They also pointed out that because marine bacteria assimilate ammonia, the possibility exists that published values of ammonia release are too low. To determine the loss due to bacterial assimilation, control experiments were conducted without animals. Fixed

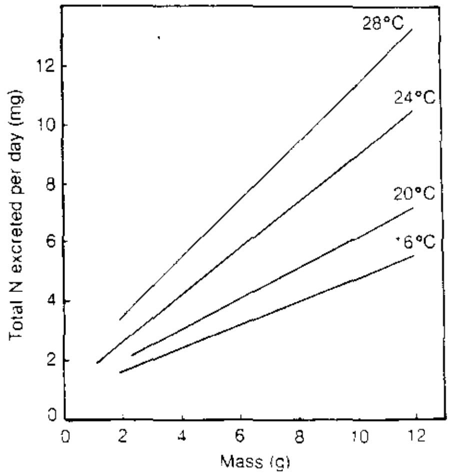

Fig. 1. Excretion of *P. indicus* at 28°C ($y = 0.98x + 1.53$; $n = 29$, $r = 0.93$), 24°C ($y = 0.79x + 1.07$; $n = 21$, $r = 0.57$), 20°C ($y = 0.51x + 0.98$; $n = 22$, $r_1 = 0.83$) and 16°C ($y = 0.39x + 0.89$; $n = 20$, $r = 0.86$), where x is the fresh mass in grams of 1 – 12 g animals and y is the total nitrogen excreted per day in milligrams.