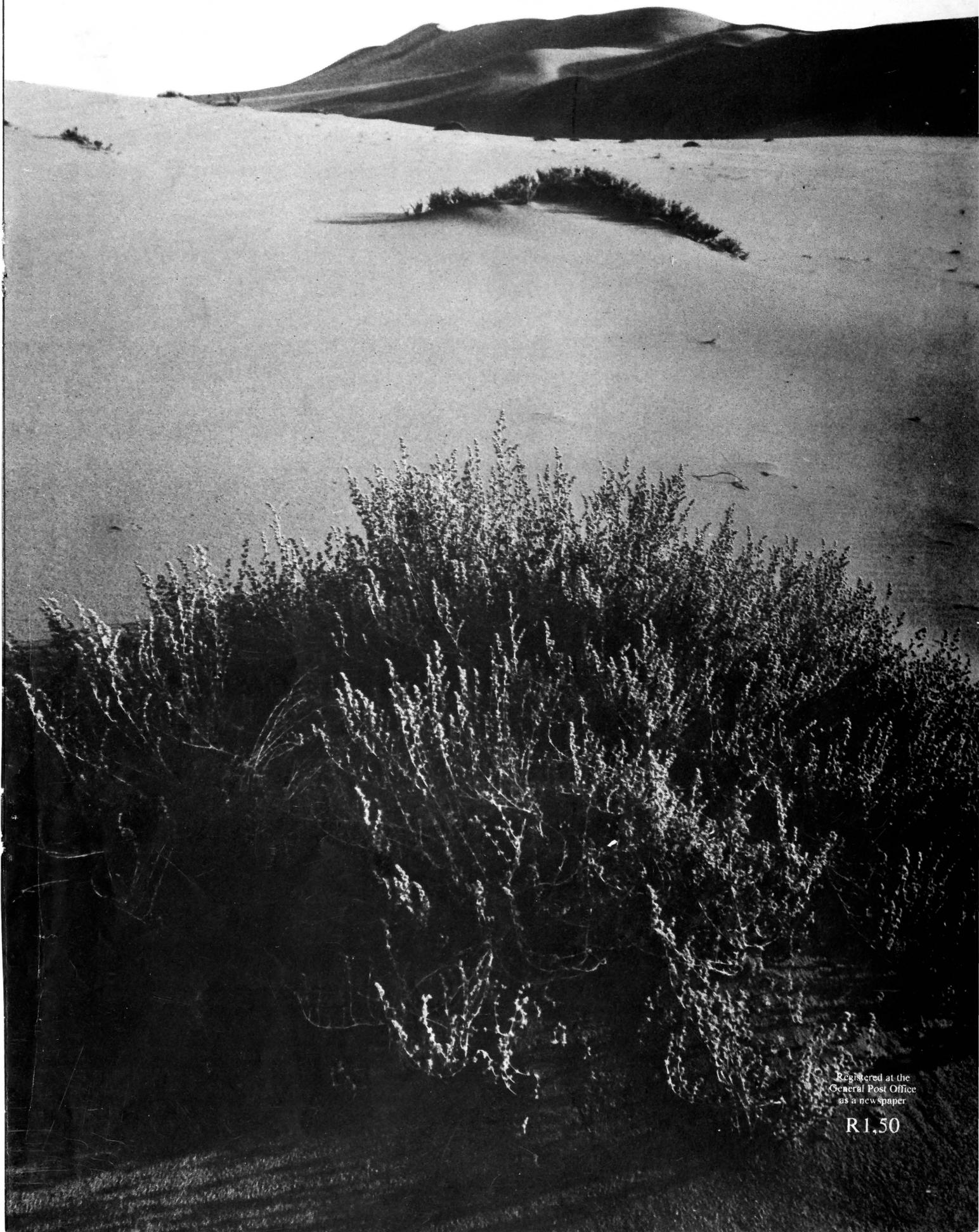


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Fog Imbibition, Satellite Fauna and Unusual Leaf Structure in a Namib Desert Dune Plant *Trianthema hereroensis*

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The plant Trianthema hereroensis, which is endemic to the Namib Desert, has been shown to absorb tritiated water rapidly through its leaves and translocate the labelled water to the root system. The unusual leaf structure and the associated satellite fauna have been described.

Daar is bewys dat Trianthema hereroensis, 'n endemiese plant in die Namib duine, getritieerde water vinnig deur die blare opneem, waarvandaan dit na die wortelsisteem vervoer word. Die buitengewone blaaranatomie sowel as die satelliet fauna, word ook beskryf.

The *Trianthema* genus (Aizoaceae) enjoys a wide distribution¹, but *Trianthema hereroensis* is restricted to the western half of the southern Namib dune system.² This area is characterised by frequent but irregular occurrence of advective fog and extremely low rainfall (15–22 mm annual average).^{3,4} Moreover, the *Trianthema* plants, which occur on the dune bases and sand-covered areas in the interdune valleys (Fig. 1), are frequently the only living plants, apart from the grass *Stipagrostis sabulicola*, which continue to grow and survive indefinitely in this area for prolonged periods without rain. As such, they represent an important source of nutrition and shelter for a surprisingly large variety of satellite desert animals and for this reason we



Fig. 1. *Trianthena hereroensis* growing within its typical habitat.

considered it essential to investigate the survival strategies employed by this unusual plant in its apparently harsh and hostile environment. The other plant which occurs sympatrically with *T. hereroensis*, *Stipagrostis sabulicola*, also survives long periods without rain but does not continue to flower and produce seed throughout the year nor does it support the variety of animals as does *T. hereroensis*.

Procedure

The investigation had three main goals. Firstly, in view of the frequent condensation of fog water upon the plants, we wished to establish if they were capable of swift absorption of water through the leaves and then translocation of this water to the rest of the plant. Secondly, we were interested in finding out whether the micro-anatomy of the leaves was adapted to either facilitating water absorption or preventing excessive water loss. Finally, we also wished to establish the nature of the satellite fauna which is associated with this species, to elucidate in part the functional ecology of this species.

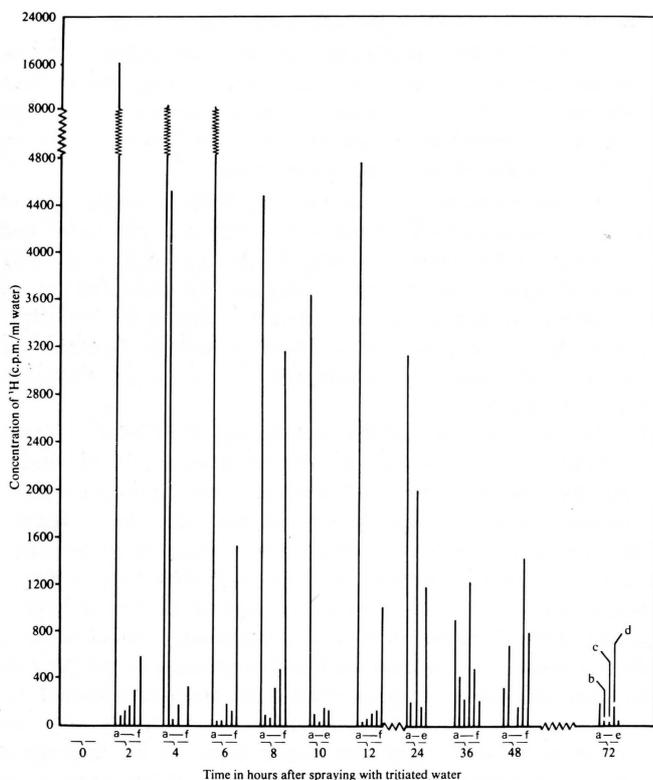


Fig. 2. The distribution of tritiated water (TOH) in individual plants which have been sampled at the indicated time intervals after spraying with TOH. Leaf samples are indicated as *a* and root tip samples as *f*, while intermediate samples at *c*. 6 cm intervals are indicated by *b*, *c*, *d*, and *e*.

To assess the water-absorbing capacity of the leaves, 10 actively growing plants were selected which were fairly uniform in size and occupied the typical micro-habitat of the species. The wind-blown sand was cleared away from the main stem of each plant and a polyethylene sheet was attached to the stem in such a way as to prevent any tritiated water (TOH), which was sprayed on the leaves, from reaching the root system. Each plant was then aerosol-sprayed with 25 cm³ of TOH (37 μCi/25 cm³) at 06h15, when cool conditions prevailed. Individual plants were then excavated at increasing intervals after spraying, namely, one at 2h, 4h, 6h, 8h, 10h, 12h, 24h, 36h, 48h, and one at 72h. When the first sample was taken all surface moisture from the spraying procedure had disappeared.

Immediately after removal of the plant, representative tissue samples were removed from the leaves and at approximately 0.6-cm intervals along the stem to the tip of one root. These samples were immediately placed in a scintillation vial, sealed and frozen for later analysis. This procedure usually provided 6 samples from each plant. On arrival in the laboratory the tissue samples were subjected to vacuum-sublimation and the resulting water distillate was mixed with scintillation fluid (Hewlett Packard's Insta Gel) and finally counted in a scintillation counter. Suitable precautions were taken while collecting the tissue samples to prevent cross-contamination. During the same period leaf tissue samples were collected from unsprayed plants and fixed for later routine sectioning and staining.

To examine the satellite fauna associated with this species, 5 entire plants were excavated, weighed and the satellite fauna was collected, weighed and identified. In addition, 0.5 m³ of sand surrounding each plant was carefully sifted and again all animals were collected, weighed and identified.

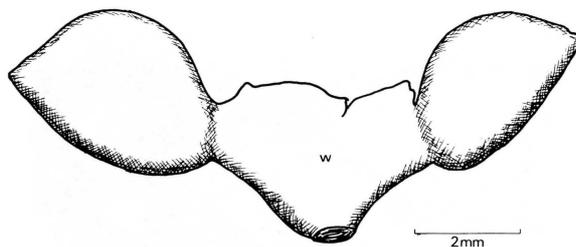


Fig. 3. Side view of two opposite leaves of *Trianthena hereroensis* showing fused petiolar wings (*w*).

Results and discussion

The results of the spraying experiments are summarised in Fig. 2. They show that the labelled water was rapidly absorbed by the leaves and after only two hours, significant amounts were recorded in the root tips. It also appears as if, with increasing time, the TOH became more uniformly distributed throughout the plant. The overall reduction in TOH concentration with time suggests that water turnover in these plants is fairly rapid, which is surprising for a desert-adapted plant. It should, however, be remembered that different individuals were sampled at each time interval and that individual variation in the size of the absorptive surface would influence the latter results considerably.

It would appear therefore that *T. hereroensis* is capable of rapid water absorption through the leaves and translocation of this water through the root system. This indicates that these plants are able to make very efficient use of the irregular condensing fogs which are characteristic of its habitat. It does not, however, imply that they are solely dependent on fog water as we found that the extensive root system is in direct contact with damp sand at the base of the dunes. Nevertheless, if the restricted distribution of this species within the western duen system is taken into account, the dependence upon fog water appears to be more critical than utilization of soil moisture, because the plants only occur within approximately 50 km of the

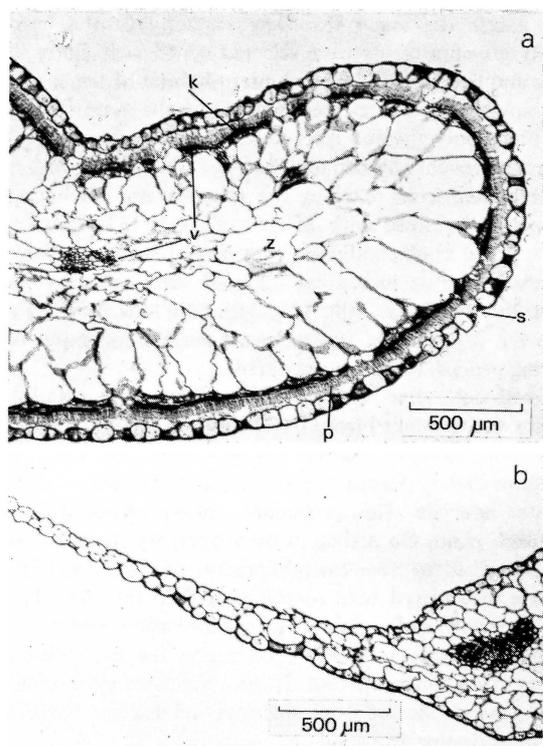


Fig. 4. a. Cross-section through part of a leaf blade of *Trianthema hereroensis*. b. Cross-section through half of a winged petiole; k, Kranz sheath; p, palisade layer; s, stoma; v, veins; w, petiolar wing; z, water-storing parenchyma.

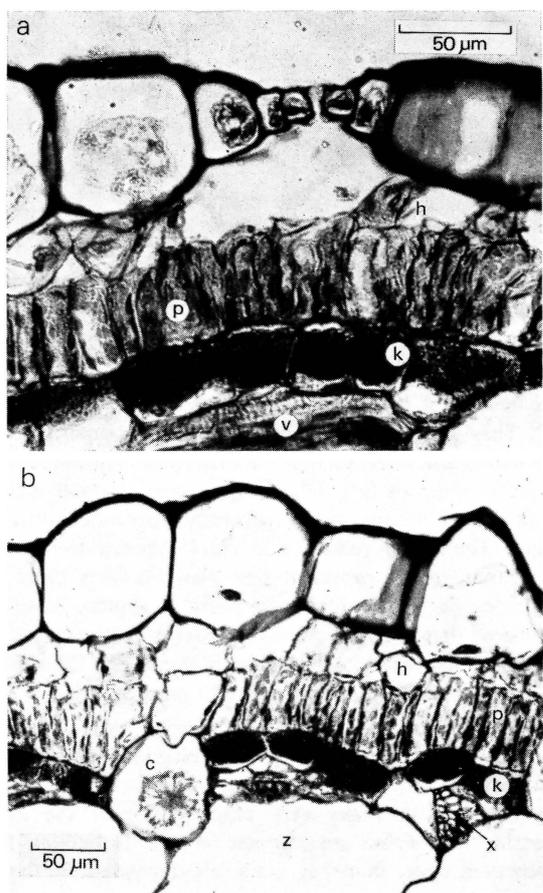


Fig. 5. a. Stoma of *Trianthema hereroensis* and adjoining tissues; b. Kranz sheath and adjoining tissues; c. crystal of calcium oxalate; h, subepidermal parenchyma; k, Kranz sheath; p, palisade parenchyma; v, vein; x, xylem; z, water-storing parenchyma.

coast where fog is most frequent. In the eastern half of the dune system, fog is less frequent but rainfall is considerably greater thus providing in all likelihood a higher soil moisture gradient; but the plants do not occur in this area. A final possibility which should be considered is that within the fog belt the plant may be able to make efficient use of fog in two ways. Firstly, by direct absorption through the leaves and, secondly, during a heavy condensing fog, water would drip freely from the plant and percolate beneath the sand where it could be absorbed through the root system. In the latter case the shading effect of the plant would contribute significantly to conservation of soil moisture.

This ability to absorb leaf-surface moisture efficiently is not unique to *T. hereroensis* and has been demonstrated in another Namib-endemic species, namely *Welwitschia mirabilis*, which also occurs predominantly within the fog zone.⁵

Finally it should be noted that although *T. hereroensis* is able to flower and produce seed indefinitely without rain, often being one of only two actively surviving plants within the ecosystem, it nevertheless appears to require rain for germination.

The leaves of *T. hereroensis* are small and have short petioles with wide membranous wings. The leaf blades are highly succulent, compressed ovoids with a pointed tip (Fig. 3) and are up to 6 mm long, 5 mm wide and 3 mm thick. Microscopic examination of the leaf (Fig. 4) reveals a concentric structure. The epidermis is overlain by a thin, smooth cuticle, only 1–1.5 µm thick, overlaying a thicker outer cellulose cell wall. The thin cuticle is surprising for an "arid-adapted" plant, but may facilitate absorption of fog water. The epidermal cells are large, have large vacuoles and probably function as water-storing cells. Contrary to expectation, the stomata are not recessed beneath the surface but are level with the outer epidermal walls. The guard cells are about one quarter the height of the epidermal cells and large substomatal air-chambers are present. The inner periclinal walls of the epidermal cells have a cuticularised layer where they adjoin sub-epidermal intercellular spaces.

The mesophyll comprises four cell types (Figs 4 and 5):

1) Sub-epidermally a single layer of large thin-walled, more or less isodiametric, parenchyma cells occur. They have large vacuoles, very few chloroplasts, and are separated by large irregular inter-cellular air-spaces which probably act as an insulation against exposure to excessive heat.

2) The chlorenchyma is in the form of, firstly, a single layer of narrow, closely packed palisade cells. They are thin-walled and contain small disc-shaped chloroplasts arranged against the long anticlinal walls, in which position they are best protected against too intense irradiation. In this context it should be mentioned that the leaves were collected and fixed at midday. Occasionally this palisade layer is interrupted by a large colourless parenchyma cell.

3) The chlorenchyma of the leaf further displays the Kranz syndrome, and consists of a bundle sheath externally in contact with the palisade layer, and internally with numerous small vascular bundles. These bundle sheath cells have slightly thickened cell walls and a dense mass of ellipsoid chloroplasts. This configuration resembles the Eryngiophyllum type of Kranz which Brown⁶ demonstrated in cylindrical leaves of several genera of the Chenopodiaceae and Compositae, in which the cells form a single layer around the leaf just internal to the palisade layer and external to a ring of small veins. He concludes that this layer consists of modified mesophyll. In *T. hereroensis*, however, transverse sections show the Kranz layer to be interrupted between veins by one or a few cells devoid of chloroplasts, some of them containing a single large crystal presumably of calcium oxalate (Fig. 5). Tangential sections give the true picture: the Kranz tissue is a network closely associated with a network of small veins, and forms an incomplete bundle sheath external to every vein; the large colourless crystal-containing cells lie in

Table 1. Satellite fauna occurring on *T. hereroensis* and in the immediate vicinity of the plant. Each item listed indicates a different species.

Animal	Mean biomass (g dry mass/plant)
Coleoptera (subfamily: Cassidinae)	0.0557
Coleoptera larvae	0.0359
Family: Acrididae	0.3084
Family: Curculionidae	0.4161
Araneida	0.0007
Family: Pentatomidae	0.0043
<i>Coloborrhis corticina</i> (Hemiptera)	0.1625
Family Chrysopidae (Neuroptera)	0.0042
Family Formicidae (Hymenoptera)	0.6670
Family Coccidae (Hemiptera)	2.6316
Araneida	0.0174
Lepismatidae (Thysanura)	0.0148
Araneida	0.0442
Araneida	0.0183
Diptera	0.0125
Hymenoptera	0.0067
Araneida	0.1105
Diptera	0.0047
Lepidoptera	0.0012
Araneida	0.0044
Coleoptera (pupa)	0.0026
Superfamily: Coccoidea (Hemiptera)	0.1138
Coleoptera	0.0009
Family: Lygaidae (Hemiptera)	0.0013
Araneida	0.0002
Diptera (larva)	0.0447
Araneida	0.0014
Hemiptera	0.0007
Curculionidae	0.7306
Araneida	0.0553
Araneida	0.0024
Coleoptera	0.0031
Tenebrionidae	0.0081
Hymenoptera	0.1469
Diptera larvae	0.0100
Reptilia (<i>Meroles</i> sp.)	0.3010
Total biomass per plant	5.9441 g

the interstices of the network. Of especial interest in this respect is the hypothesis that the Kranz type of leaf anatomy and the associated C₄ metabolism represent adaptations for efficient and rapid carbon dioxide fixation in environments where water stress frequently limits photosynthesis.⁷

4) The central part of the leaf is occupied by large, thin-walled water-storing parenchyma devoid of chloroplasts. This forms the main water-storage tissue of the leaf.

The main vascular supply of the leaf comprises a single main vein and two lateral veins, embedded in the central water storing parenchyma. These veins branch into numerous small veins forming the network in contact with the Kranz cells. The small veins on the abaxial side are inverted; this means that all of the small veins have the xylem towards the outside in direct contact with the Kranz sheath, and the phloem towards the inside. The xylem placed towards the outside may possibly help in the rapid translocation of water absorbed through the leaf surface.

In order to find out in what manner the leaf of *T. hereroensis* differs from that of other species of *Trianthema* not adapted to extreme desert conditions, a cursory examination of the leaf of *T. triquetra* from the Soutpansberg, Transvaal, obtained from herbarium specimens through the courtesy of the Director of the State Herbarium in Pretoria, was carried out. Anatomically the leaf of *T. triquetra* resembles that of *T. hereroensis* in the possession of a very thin cuticle and superficial stomata, a

colourless sub-epidermal layer, one layer of palisade cells, and Kranz cells external to numerous small vascular bundles. The vascular bundles probably have the xylem and phloem inverted, as far as could be seen in the sections made with a freezing-microtome. The leaf, however, is dorsiventral, with a colourless adaxial groove, and water storage tissue is much reduced. Except for these two differences, there are no other significant anatomical differences between the leaves of the two species. Important morphological differences, however, occur: the leaves of *T. triquetra* are narrowly linear, do not protect one another, and have very narrow petiolar wings, whereas the stout, compressed ovoid leaves of *T. hereroensis* are borne in compact masses, protecting one another to some extent. The wide petiolar wings also probably help to protect the leaf groups. Furthermore, the wings of each pair of opposite leaves are fused at their bases (Fig. 3), forming a small cup-shaped structure in which fog water doubtless collects.

The survey of the satellite fauna, which occurs on and around *T. hereroensis*, showed that this species provides either nourishment or shelter to a surprisingly large variety of desert animals. This variety is reflected in the list of species presented in Table 1. These data are not complete as they only represent results obtained from examining 5 plants. For example, several other species such as the Namib gerbil *Gerbillurus paebe* is frequently seen in close association with *Trianthema*. Finally, although Table 1 shows a marked variety of animals in association with *T. hereroensis*, it should be noted that the total biomass is nonetheless very low.

Summary

Trianthema hereroensis occupies a most unusual habitat in the fog belt of the southern Namib dune system. It is also one of only two plants in this system which continue to grow, and the only plant which flowers, actively throughout the year without rain. We were able to show that *T. hereroensis* is able to absorb tritiated water rapidly through the leaves and translocate this water swiftly to the root system. Microscopic examination of the leaves revealed that the plant appears to be adapted to facilitating water absorption as well as water storage. The position of the xylem external to the phloem probably helps in the rapid translocation of fog water. In addition, the Kranz type of leaf structure, which is usually associated with C₄ metabolism, possibly enables the plant to proceed with carbon dioxide fixation in spite of water stress. Finally, a superficial survey of the satellite fauna of *T. hereroensis* showed that a remarkably large variety of desert animals are dependent upon this species for either food or shelter.

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- Dyer, R. A. (1975). *Genera of South African Flowering Plants*. Vol. 1. Government Printer, Pretoria.
- Merxmüller, H. (1966-72). *Prodromus einer Flora von Südwest-Afrika*. J. Cramer, Lehre.
- Seely, M. K. and Stuart, P. (1976). Namib Climate: 2 The climate of Gobabeb, ten year summary. *Namib Bull.*, No. 1, 7-9.
- Schulze, B. R. (1960). The climate of Gobabeb. *Sci. Pap. Namib. Des. Res. Stn.*, No. 38, 5-12.
- Bornman, C. H., Botha, C. E. J. and Nash, L. J. (1973). *Welwitschia mirabilis*: observations on movement of water and assimilates under föhn and fog conditions. *Madoqua II*, 2, 25-31.
- Brown, W. V. (1975). Variations in anatomy, associations, and origins of Kranz tissue. *Am. J. Bot.*, 62, 395-402.
- Laetsch, W. M. (1968). Chloroplast specialization in dicotyledons possessing the C₄-dicarboxylic acid pathway of photosynthetic CO₂ fixation. *Am. J. Bot.*, 55, 875-883.
- Louw, G. N. (1972). The role of advective fog in the water economy of certain Namib Desert animals. *Symp. Zool. Soc. Lond.* No. 31, 297-314.