

## Some aspects of the water relations of the lichen *Xanthomaculina hottentotta* (Ach.) Hale from the Namib desert

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The water relations of the desert lichen *Xanthomaculina hottentotta* were investigated using thermocouple psychrometry. Although the water relations of *X. hottentotta* were similar to those of other lichens from xeric habitats, *X. hottentotta* lost less K<sup>+</sup> following sudden re-wetting, contained less intercellular water and had a higher  $\psi_{\text{rs}}$  than these lichens. The implications of these findings for the water relations of *X. hottentotta* are discussed.

**Keywords:** Lichen, desiccation, thermocouple psychrometry, Namib desert.

Abbreviations:  $\epsilon_v$ : bulk modulus of elasticity;  $\psi$ : water potential;  $\psi_{\text{rs}}$ : osmotic potential at full turgor;  $\psi_p$ : turgor pressure; PV: pressure volume;  $R_a$ : apoplastic water content;  $R_s$ : symplastic water content; RWC: relative water content.

### Introduction

Desert coastal fog zones often possess unique assemblages of lichen species (Rundel 1978; Kappen 1988). While some information exists on the ecophysiological adaptations of lichens to New World fog deserts [see Lange *et al.* (1990) for references] much less is known about lichens from the Namib desert, Namibia. Rainfall in the Namib is extremely irregular, and records at Swakopmund show that the mean annual precipitation is 13 mm, which occurs one to five days per year (Wessels & van Vuuren 1986). However, fog is a frequent event along the coast, and 202–295 days every year are overcast, foggy or experience dew-fall events (Walter 1937).

The most detailed study of the ecophysiology of Namib lichens is that of Lange *et al.* (1990) on the fruticose species *Teloschistes capensis*. Results showed that dew and fog often increased thallus water contents to above 100%. This allowed net photosynthesis to take place for two to three hours in the morning before the water content of the lichens dropped below 15% and net photosynthesis ceased. However, very little is known about the basic water relations of these lichens. In response to the challenge of water shortage, many drought tolerant higher plants can display osmoregulation, i.e. reduce their osmotic potential at full turgor ( $\psi_{\text{rs}}$ ) (McKersie & Leshem 1994). The advantages of this are first that low  $\psi_{\text{rs}}$  will reduce the relative water content (RWC) at which turgor is lost. Second, low  $\psi_{\text{rs}}$  will reduce the water potential ( $\psi$ ) of the plant at turgor loss, thus creating a steeper gradient for the uptake of water from the soil. In addition, Radin (1983) suggested that, for higher plants, a low tissue bulk modulus of elasticity ( $\epsilon_v$ ) and a low apoplastic water fraction may improve drought tolerance by reducing RWC at turgor loss. Preliminary observations of Beckett (1995) showed that lichens from xeric microhabitats tended to have lower values of  $\psi_{\text{rs}}$ ,  $\epsilon_v$  and apoplastic water fraction than lichens from more mesic microhabitats. As a result, they lost turgor at lower RWCs. The objective of the present investigation was to examine the water relations of the desert lichen *Xanthomaculina hottentotta*, and to compare results with those obtained for other lichen species. In particular, the aim was to test if the RWC of this species at turgor loss was significantly lower than values obtained from other lichens, and if so how *X. hottentotta* achieves this.

### Materials and Methods

#### Plant material

Material of the umbilicate lichen *Xanthomaculina hottentotta* (Ach.) Hale was collected from rocky outcrops near the Desert Ecological Research Unit of Namibia, Namib-Naukluft Park, Namibia. Plants were stored air dry for 4 days, then hydrated by first storing them at a relative humidity of 100% (in a desiccator over distilled water) at 20°C and a light intensity of 135  $\mu\text{moles m}^{-2} \text{s}^{-1}$  for two days, then placing them in distilled water for 1 h. Lichens showed very little increase in weight after this time and were, therefore, assumed to be fully turgid.

#### Determination of thallus water potential and its components and the cellular location of thallus water

The definition of RWC varies between workers, but here is defined as:

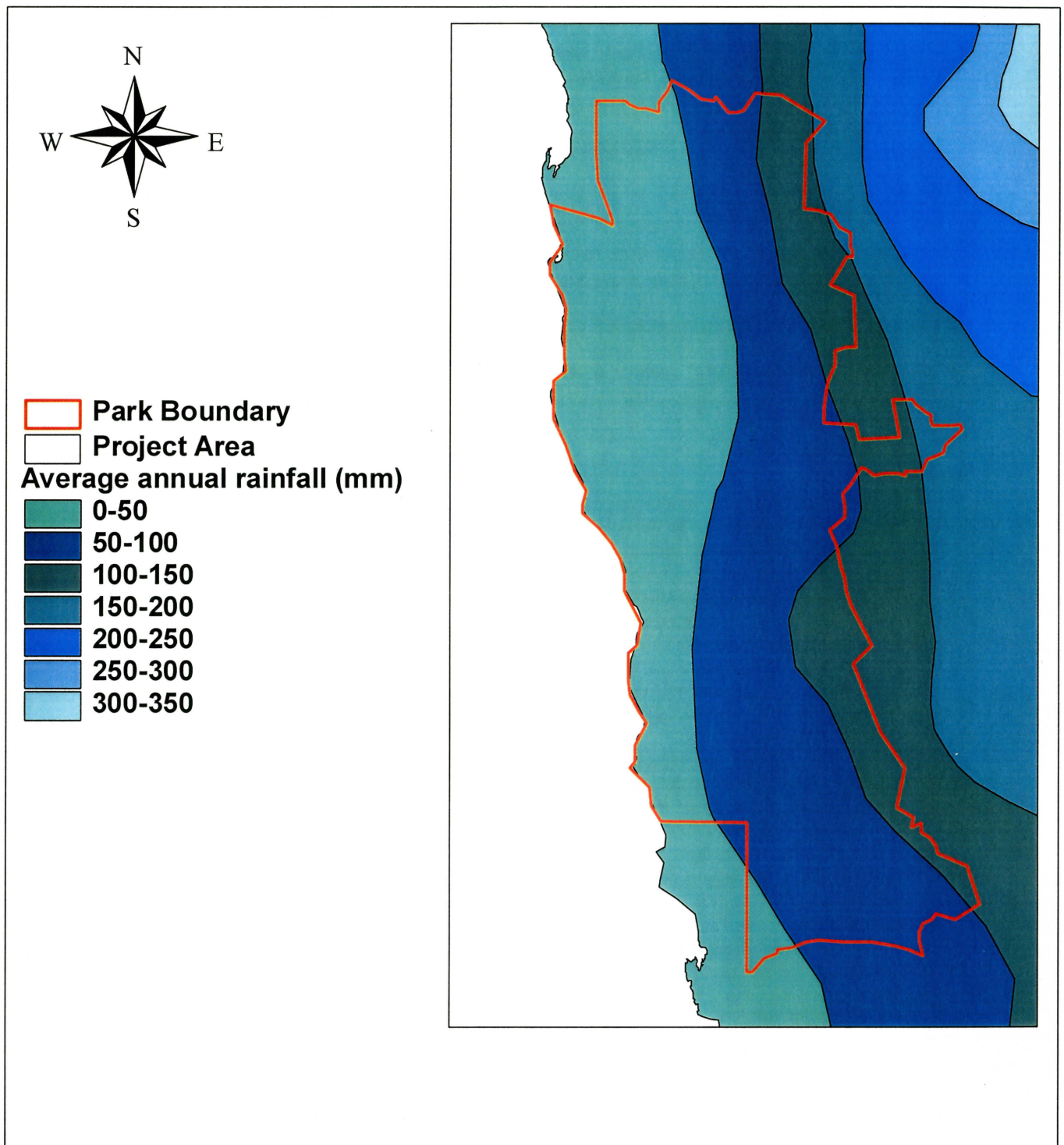
$$\text{RWC} = \frac{\text{FW} - \text{DW}}{\text{FT} - \text{DW}}$$

where FW is the fresh mass of the samples for a given measurement, DW is the dry mass and FT is the turgid mass. Thallus water potential was determined using a Decagon SC-10A thermocouple psychrometer linked to a Wescor HR-33T microvoltmeter. After equilibration for 4 h and measurement of c. 100 mg of hydrated material, the plants were allowed to lose between two and three mg of water, and after 4 h  $\psi$  was again measured. This was repeated until the plants had reached a RWC of c. 0.5 and a  $\psi$  of c. -4 MPa. After this, the equilibration time was increased to 12 h, and measurements were repeated until the plants reached a RWC of 0.25 and a  $\psi$  of c. -12 MPa. In total, 25 measurements were made on each of five samples. Standard solutions of known  $\psi$  were always run with samples, and values of corrected to a temperature of 20°C.

Water in lichens can occur in the symplast or in the apoplast, i.e. the pores in the cell wall and the symbols  $R_s$  and  $R_a$  indicate the proportion of water in a fully hydrated thallus in these two fractions respectively. To estimate  $R_a$  a pressure-volume (PV) curve, i.e. (-1/ $\psi$ ) as a function of (1 - RWC), was drawn. The resulting curve was initially concave, but beyond the region where turgor was lost (i.e. where turgor no longer contributed to  $\psi$  the curve became linear (Figure 1A). From the PV curve turgor potential ( $\psi_p$ ) was calculated as the difference between the extrapolated linear portion of the curve

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3.2.1.a The presence of the cold Benguela upwelling system lying along the eastern Atlantic coast dominates the climate of the Namib-Naukluft Park. As a consequence all the relevant isohyets run predominantly north-south. Rainfall in the park increases from less than 20 mm per year on the west coast to approximately 2000 mm per year in the Naukluft Mountains in the east. Great inter- and intra-annual variation prevails in this arid area.

**Table 1** Thallus K<sup>+</sup> contents, K<sup>+</sup> lost on re-wetting and characteristics of the water relations the lichen *Xanthomaculina hottentotta* from the Namib desert compared with values obtained for lichen species from other habitats. Figures are given  $\pm$  one standard deviation, n = 5

	<i>Xanthomaculina hottentotta</i>	Mean of four mesic species*	Mean of four xeric species*	Mean of two maritime species#
Thallus K <sup>+</sup> content ( $\mu\text{mol g}^{-1}$ dry mass)	50 $\pm$ 3	324	73	47
K <sup>+</sup> lost on re-wetting (% intracellular)	6.0 $\pm$ 2.5	26	12	12
$\Psi_{\pi s}$ (MPa) (estimated from PV curve)	-1.69 $\pm$ 0.12	-1.57	-2.36	-2.42
$\Psi_{\pi s}$ (MPa) (estimated from freezing)	-1.25 $\pm$ 0.01	-1.76	-2.36	-2.83
Mean $\Psi_{\pi s}$ (MPa)	-1.47	-1.66	-2.36	-2.63
K <sup>+</sup> concentration of protoplasm (mM)	49 $\pm$ 1	222	89	64
$\Psi_{\pi s}$ due to K <sup>+</sup> (%)	11 $\pm$ 0	60	17	8
Thallus H <sub>2</sub> O content (g g <sup>-1</sup> dry mass)	1.19 $\pm$ 0.03	2.22	1.17	1.13
Intercellular thallus H <sub>2</sub> O	0	0.15	0.19	0.25
Apoplasmic thallus H <sub>2</sub> O (R <sub>a</sub> )	0.14 $\pm$ 0.01	0.23	0.13	0.17
$\epsilon_v$ at $\Psi_p = 1$ MPa (MPa)	2.2 $\pm$ 1.8	4.0	1.8	3.8
RWC at turgor loss	0.41 $\pm$ 0.03	0.53	0.45	0.44

\*Taken from Beckett (1995)

#Taken from Beckett (1996b,c)

and the actual curve. R<sub>a</sub> was calculated as the X-axis intercept of the linear part of the curve, i.e. the water content of the thallus at very low water potentials. As this water occurs in small (5 to 10 nm in diameter) pores in the cell walls, lichens will only lose this water when the thallus is very dry and  $\psi$  less than 15 MPa (Meidner & Sheriff 1976). Osmotic potential at full turgor ( $\psi_{\pi s}$ ) was calculated from the Y-axis intercept, i.e. the value of  $\psi_{\pi}$  at 100% RWC (Tyree & Jarvis 1981). Tissue elasticity ( $\epsilon_v$ ) was calculated from the relationship between turgor potential ( $\psi_p$ ) and RWC (Stadelmann 1984).

As a check on the estimate of  $\psi_{\pi s}$  derived from the PV curve, the  $\psi_{\pi}$  of 5 replicate samples were estimated as follows. Lichen tissue (100 mg) was rehydrated as described above and placed in the sample cups, wrapped in at least three layers of 'Parafilm' and immersed in liquid nitrogen for c. 5 minutes. The cups were then allowed to warm to room temperature (c. 1 h). The Parafilm was then removed, and the sample cups rapidly transferred back to the thermocouple psychrometer. After an equilibration time of 1 h  $\psi$  was determined. Assuming freezing ruptures membranes and thus destroys turgor,  $\psi$  will equal  $\psi_{\pi}$ . This method underestimates  $\psi_{\pi}$  because apoplasmic water dilutes ions and molecules in the symplast. To correct for this, the equation of Jones and Rawson (1979) was used:

$$\psi_{\pi s} = \frac{\psi_{\pi k}}{1 - R_a}$$

where  $\psi_{\pi k}$  is the water potential of water-saturated killed lichens.

#### Determination of the cellular location of K<sup>+</sup> and an index of desiccation tolerance

A simplification of the method of Buck and Brown (1979) was used to estimate the cellular location of K<sup>+</sup> and an index of desiccation tolerance. This involved keeping two sets of four replicates of 100 mg of lichen tissue at 0% and 100% relative humidity (RH) for 48 h. Sudden re-wetting was simulated by shaking lichen samples in 10 ml of distilled water for 0.5 h. They were then transferred to 10 ml of NiCl<sub>2</sub> for 0.5 h to displace cell wall bound cations. Finally, they were shaken in 10 ml of 1 M HNO<sub>3</sub> for 1 h to release intracellular

K<sup>+</sup>. The concentrations of K<sup>+</sup> in the elutions were determined by atomic absorption spectrophotometry. K<sup>+</sup> leakage caused by desiccation was estimated as:

$$\frac{\text{intracellular [K] of lichens pretreated at 100\% RH} - \text{that at 0\% RH}}{\text{intracellular [K] of lichens pretreated at 100\% RH}}$$

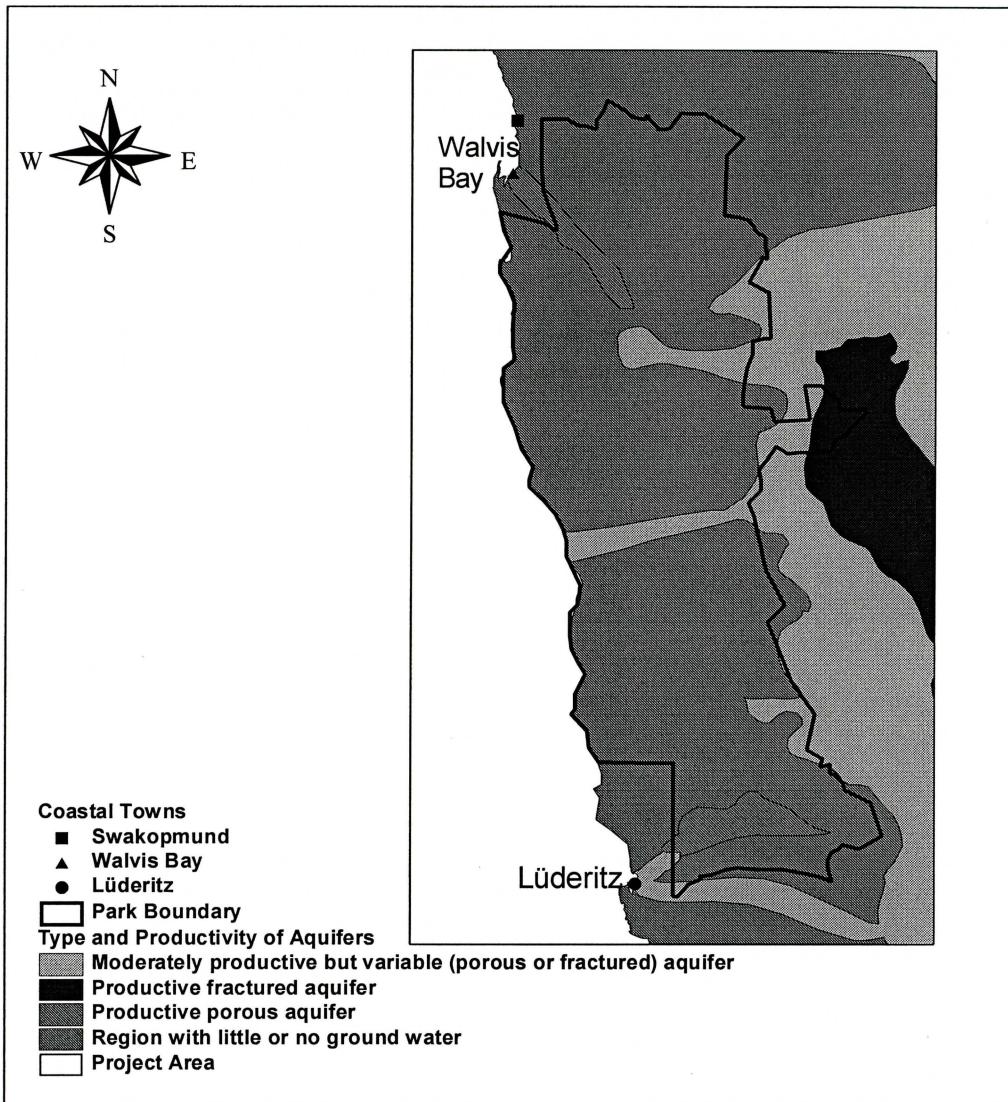
[see Buck and Brown (1979) for discussion on the use of K<sup>+</sup> leakage as an index of desiccation tolerance]. The mean concentration of K<sup>+</sup> (mol l<sup>-1</sup>) in the cytoplasm was calculated as follows:

$$\frac{\text{mean intracellular thallus K concentration (mol g dry mass}^{-1}) \times 100}{\text{mean thallus H}_2\text{O content (g g dry mass}^{-1}) \times (1 - R_a)}$$

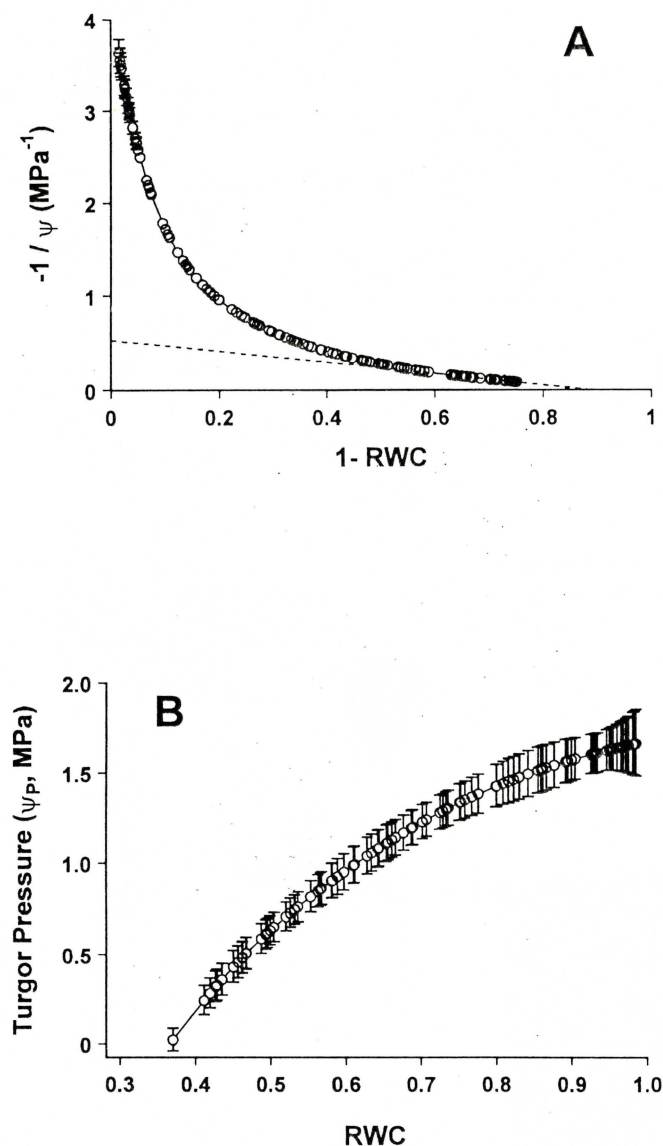
The  $\psi_{\pi}$  of a solution of KCl of this concentration was determined from tables, and expressed as a percentage of  $\psi_{\pi s}$ , estimated as the mean of the values derived from the PV curve and the freezing methods.

#### Results and Discussion

Table 1 presents a summary of the results obtained in this study. *Xanthomaculina hottentotta* is clearly an extremely desiccation tolerant lichen. Sudden re-wetting only induced a loss of 6% of intracellular K<sup>+</sup> compared with the 26% reported by Beckett (1995) for lichens from mesic microhabitats (Table 1). Plotting (-1/ $\psi$ ) as a function of (1 - RWC) resulted in a normal PV curve (Figure 1A). As the RWC of the lichen fell,  $\psi_p$  declined (Figure 1B). It is interesting that in almost all the species studied by Beckett (1995, 1996a,b,c)  $\psi_p$  initially remained constant as the RWC decreased, only falling when the RWC of the lichens reached 0.7 to 0.8. Beckett (1996a) described this behaviour in detail, and suggested that as fully hydrated lichens dry, they initially lose intercellular water, and turgor only decreases when the plants start losing symplasmic water. Results presented here indicate that *X. hottentotta* only contains small quantities of intercellular water. Speculating on the ecological significance of this finding is difficult. However, workers often observe reduced



3.2.5 c Much of the Namib-Naukluft Park is underlain by little or no ground water. The aquifers used to supply Walvis Bay and Luderitz are the most productive in the park.



**Figure 1** A. Pressure volume curve of *Xanthomaculina hottentotta*. B. Turgor potential as a function of RWC in *X. hottentotta*. Turgor potential was calculated as the difference between the extrapolated linear portion of the PV curve and the curve. In this Figure points represent fitted values with 95% confidence limits calculated using the 'Spline' program of Hunt and Parsons (1974).

rates of photosynthesis in fully hydrated lichens [for review see Kershaw (1985)]. This suggests that filling of intercellular pores with water increases the diffusive resistance of CO<sub>2</sub> to the photobionts. Desert lichens are usually only metabolically active for a very short time, and reducing the capacity of a thallus to hold intercellular water may reduce the risk of photosynthetic depression.

It seems likely that at least some water in a fully hydrated thallus of *X. hottentotta* is intercellular. This is because first, although  $\psi_p$  fell as the RWC declined (Figure 1B), the shape of the graph did not closely resemble relationships normally reported in the literature for higher plants (e.g. Robichaux 1984; Stadelmann 1984). Specifically,  $\psi_p$  did not fall rapidly at high RWCs, suggesting that some of the first water lost from the lichen may have been from intercellular pores rather than the symplast. Second, the estimate of  $\psi_{\pi s}$  derived from freezing the tissue was higher than that derived from the PV curve (Table 1), suggesting that intercellular water may have diluted

protoplasmic sap. If present, however, intercellular water existed in smaller quantities than in the species examined by Beckett (1995, 1996a,b,c).

In many respects, the water relations of *X. hottentotta* resembled those of other lichens growing in xeric microhabitats (Table 1), but *X. hottentotta* had a much higher  $\psi_{\pi s}$  than these lichens. The reasons for the high value of  $\psi_{\pi s}$  in *X. hottentotta* are unclear. However, while this would normally mean that turgor would be lost at higher RWCs (Radin 1983), the desert species also had low values of  $R_a$  and  $\epsilon_v$ . As a result, plants lost turgor at similar RWCs to maritime lichens and lichens from xeric microhabitats. PV curves can be used to determine the minimum RWC needed for positive turgor. For *X. hottentotta* this value is 0.4 corresponding to a water content of about 48%. The observation of Lange *et al.* (1990) suggests that net photosynthesis can occur down to water contents of 15% in the lichen *Teloschistes capensis* that occurs in similar sites in the Namib. If the same were true for *X. hottentotta*, and assuming that *T. capensis* and *X. hottentotta* contain similar amounts of water at full hydration, this would suggest that net photosynthesis can take place when most of the cells in the lichen thallus have no turgor. It may be relevant that Scheidegger *et al.* (1995) showed that in many lichen species even collapsed photobiont cells can display net photosynthesis. This suggests that less time exists for growth, which normally requires positive turgor, than for net photosynthesis. However, *X. hottentotta* appeared to possess effective turgor maintenance mechanisms.

The K<sup>+</sup> concentration of the protoplasm of *X. hottentotta* was very low, and K<sup>+</sup> only contributed about 11% of  $\psi_{\pi s}$ . This suggests that organic molecules were probably responsible for most of the  $\psi_{\pi s}$  of *X. hottentotta*. No attempt was made to identify these molecules in this study, but recent surveys of lichens suggest that they contain high concentrations of sugars and polyols (Roser *et al.* 1992). High concentrations of sugars may protect membranes from the high concentrations of ions that occur in desiccated tissues (Bewley & Krochko 1981; Gaff 1997).

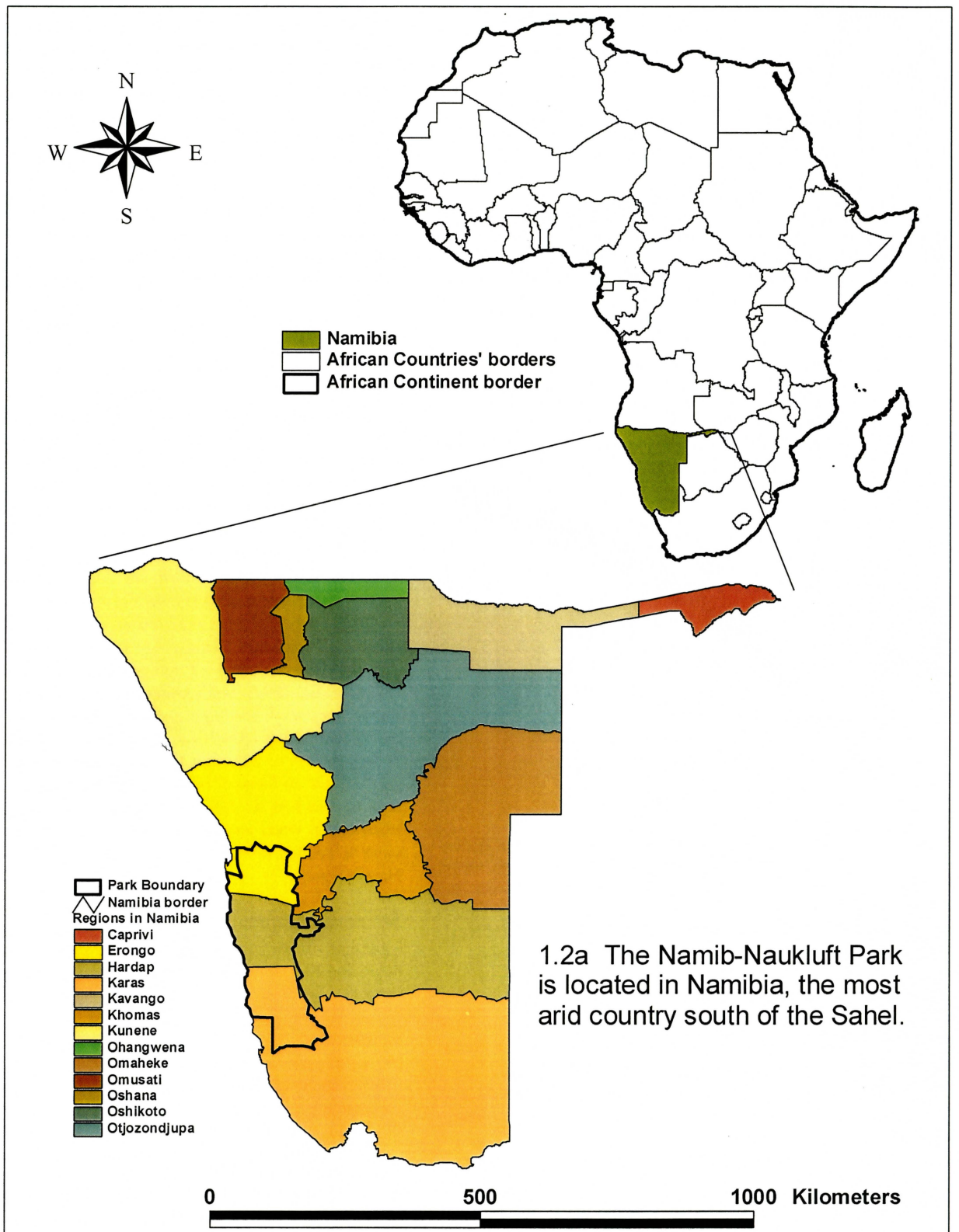
In conclusion, although the water relations of *X. hottentotta* were similar to those of other lichens from xeric habitats, *X. hottentotta* lost less K<sup>+</sup> following sudden rewetting, contained less intercellular water and had a higher  $\psi_{\pi s}$  than these lichens. More work is needed to establish if *X. hottentotta* is typical of other Namib lichens.

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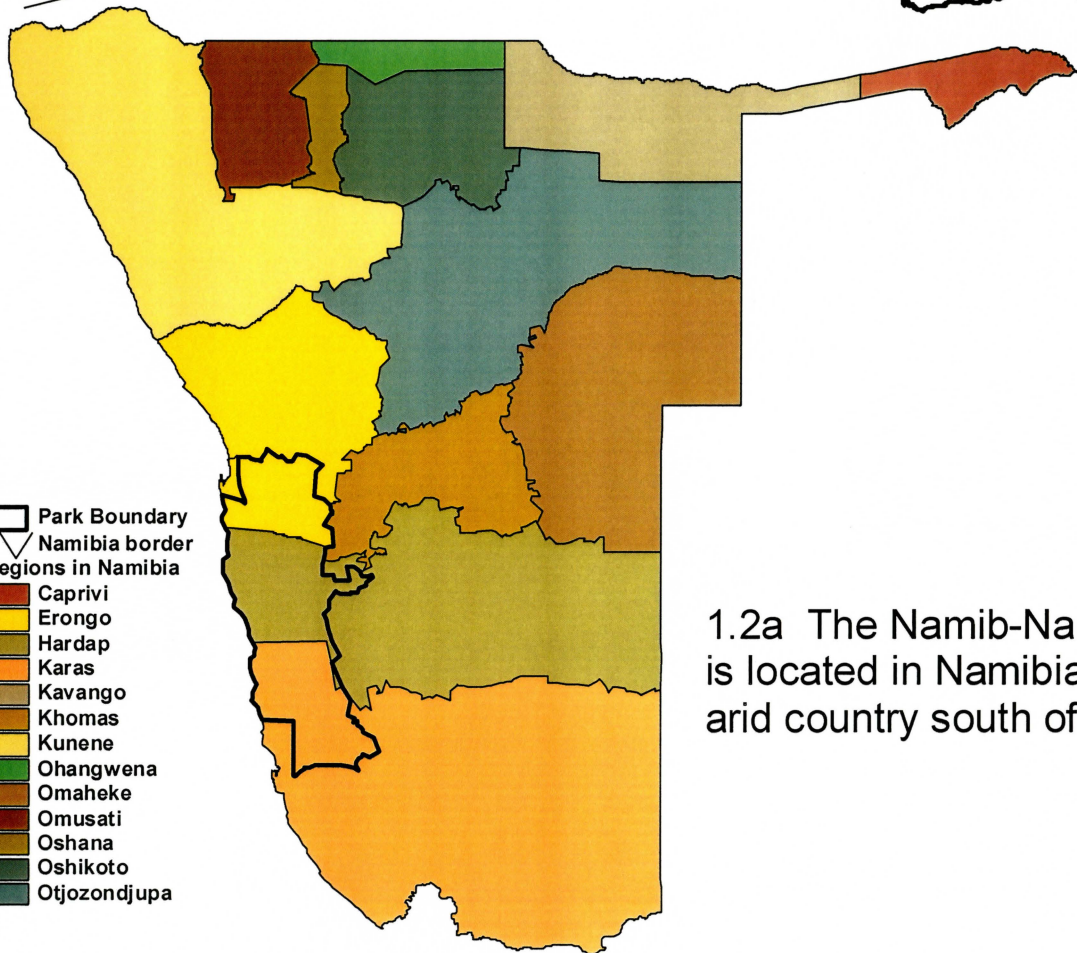
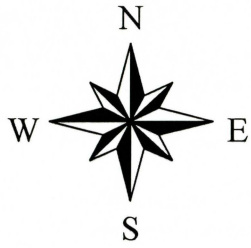
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1.2a The Namib-Naukluft Park is located in Namibia, the most arid country south of the Sahel.

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