

Morphological effects on the water balance of Antarctic foliose and fruticose lichens

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Abstract: Uptake and loss of water by six lichen species from the Argentine Islands, Antarctic Peninsula, were studied in their natural habitat and in laboratory studies. Under field conditions, during a period of rain, uptake of moisture ranged from 15% d w h⁻¹ for *Usnea antarctica* to almost 90% for *Mastodia tessellata*. Loss rates after the rain ceased were lower than the uptake rates and ranged from 8.5% d w h⁻¹ in *Umbilicaria decussata* to 38.8% in *M. tessellata*. A comparison of thalli of *M. tessellata* from the shoreline with thalli collected further inland showed significant differences in maximum water content and in rates of water loss and uptake between thalli from these sites, which could be ascribed to the presence of salt in the thalli of *M. tessellata* from the shore. Thallus samples of *Usnea antarctica* collected from an exposed site showed lower uptake rates and higher loss rates of water than samples collected from a more sheltered site. Under laboratory conditions the maximum moisture content ranged from 67% in *Usnea antarctica* to 391% in *M. tessellata*. Exposed to an atmosphere of c. 40% relative humidity and c. 15°C, lichen thalli lost their water during the first hour of the experiment at rates ranging from 34% of the maximum moisture content in *Umbilicaria propagulifera* to 70% in *U. decussata*. Rates of water loss diminished with time, and after 4–6 hours equilibrium was reached, with water contents of 14–16% of thallus dry weight. The microclimate is the driving force for the thallus water regime. Specific differences in rates of water loss and water uptake depend on the morphology and anatomy of the lichen thalli. The results of the laboratory experiments agree with those from the field study. However, local differences in microclimatic or other environmental factors can be responsible for significant differences in the water regime of thalli of the same species, a result which can only be obtained from field studies.

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Introduction

Lichen physiology is closely tied to the moisture status of the thallus (e.g. Kershaw 1985, Kappen *et al.* 1987, 1988, V.R. Smith 1988, and others). As lichens are poikilohydric – they do not appear to have active ways to influence water uptake or loss (Henssen & Jahns 1974) – thallus water content is strongly related to microclimatic conditions (Bölter *et al.* 1989). As a consequence water availability is regarded as a very important factor determining the distribution of lichens on a regional as well as on a local scale (Kappen 1985a, Longton 1988, Melick *et al.* 1994, R.I.L. Smith 1988). Hancock & Seppelt (1988) suggested that lichen species might exhibit niche specificity related to moisture availability.

Size, morphology and anatomy of the lichen thallus may influence the rates of water uptake and loss (Larson & Kershaw 1976, Larson 1979, 1981, 1984, Snelgar *et al.* 1981, Jahns 1984, Harrisson *et al.* 1986, 1989, Hancock & Seppelt 1988, Sancho & Kappen 1989, Hestmark 1992). In some of these studies size and shape of the thallus were determined using morphological or anatomical parameters

or more elaborate methods to determine surface to weight ratio (Larson and Kershaw 1976, Larson 1979, 1981, 1984).

Many laboratory studies on the water relations of lichens have been performed by spraying the thalli (e.g. Kappen *et al.* 1980, Snelgar *et al.* 1981, Kappen 1985b, Lange & Kilian 1985), by applying artificial rain or fog in a wind tunnel (Larson 1979, 1981, 1984) or by placing the thalli in an environment with controlled air humidity (e.g. Kappen & Redon 1987, R.I.L. Smith 1988).

Relatively few studies deal with water relations of lichens in natural habitats (Heatwole 1966, Lange *et al.* 1970, Kershaw & Rouse 1971, Jahns & Ott 1983) and even fewer have been performed in Antarctic habitats (Kappen 1983, Kappen *et al.* 1981).

In this paper we compare laboratory and field data on changes in water content of foliose and fruticose species to assess if laboratory data are a good guide to field performance. In addition the water uptake and loss rates are related to the morphology of the species using simple morphometric parameters.

Materials and methods

The study was undertaken during the summer of 1990/91 at the British Antarctic Survey Faraday Station on Galindez Island (Argentine Islands, 65°15'S, 64°16'W). For a general description of the geography and climate of the islands see Smith & Corner (1973) and Gremmen *et al.* (1994).

For both the field and the laboratory studies samples of four foliose and two fruticose species (Table I) were collected from a rock outcrop with well developed lichen vegetation 10 m away from the shoreline and 50 m NE of Faraday Station. All six species were collected from the north facing slope with an additional collection of *Usnea antarctica* from the south facing slope.

For the laboratory study samples of two additional fruticose species, (*Usnea aurantiaco-atra* and *Pseudephebe minuscula*), were collected near Woozle Hill, Galindez Island, 30 m above sea level and about 200 m from the shoreline. These were not included in the field study, as the distance of this site from the laboratory precluded rapid processing of the samples. Additional samples of *Mastodia tessellata* were collected from a site strongly influenced by sea spray about 2 m above main sea level and 5 m away from the shoreline (Table I).

Field studies

To measure field water content samples were lightly shaken to remove excess water, weighed immediately, and again after drying at 80°C to constant weight. However, processing limitations meant that there are not data for all species at each sample time. Five replicates of each of the species were collected every two hours except during periods of

precipitation. Because of this a statistical analysis was not possible; only standard errors of the mean are reported.

Meteorological data from the Station provided relative humidity of the air, periods of precipitation and wind speed.

Laboratory experiments

To establish rates of water uptake and loss some 20 thallus samples of different sizes of each species were collected from different places within the community. Extremely stunted thalli, thalli from very sheltered sites, very small or unusually large thalli were avoided. Extraneous matter was carefully removed and each sample was attached to a thin metal wire, carrying a numbered label. The samples were then placed in a transparent container with a saturated atmosphere. After one day the thalli were weighed on a Sartorius 1475-MP8 electronic balance, and placed in a room at 30–40% RH, and 12–17°C. The thalli were weighed after 0.5, 1, 1.5, 2, 3, 6, 12 and 24 h. After 24 hours the thalli were placed in a humid chamber at 95–100% RH and 10°C, and weighed again after 24, 48, and in some cases after 160 h. Finally dry weight was determined after drying in an oven at 80°C to constant weight.

The significance of differences between each two species was tested using ANOVA.

Morphometrical measurements

The ratio between thallus surface area and thallus volume was determined for all species. The lichen thalli were modeled as cylinders. The surface area of the lichen was estimated as the sum of the upper surface projection, the

Table I. List of species studied, with short notes on their morphology and the collection sites.

Species name	Short description
<i>Mastodia tessellata</i> (Hook.f. et Harv.) Hook.f. et Harv.	Foliose thallus, polyphyllous, up to 1.5 cm in diameter. Collected from a population about 2m from the shoreline and from the north facing slope of the rock outcrop, further inland.
<i>Pseudephebe minuscula</i> (Nyl. ex Arnold) Brodo et Hawksw.	Fruticose thallus, consisting of very thin branches, forming dense mats. Collected for laboratory experiments only, from a north facing slope at Woozle Hill, Galindez Island.
<i>Pseudephebe pubescens</i> (L.) Choisy	Fruticose thallus, consisting of thin branches, loosely entangled. Collected for field and laboratory studies from the north facing slope of the rock outcrop.
<i>Umbilicaria decussata</i> (Vill.) Zahlbr.	Foliose thallus, uniphyllous, up to 3 cm in diameter, without rhizines. Collected for field and laboratory studies from the north facing slope of the rock outcrop.
<i>Umbilicaria propagulifera</i> (Vain.) Llano	Foliose species, polyphyllous, up to 3 cm in diameter, ventral surface densely covered by rhizines. Collected for field and laboratory studies from the north facing slope of the rock outcrop.
<i>Umbilicaria antarctica</i> Frey et Lamb	Foliose species, uniphyllous, up to 30 cm in diameter, ventral side partly covered by rhizines. Collected for field and laboratory studies from the north facing slope of the rock outcrop.
<i>Usnea antarctica</i> Du Rietz	Fruticose thallus. Collected for field and laboratory studies from both the north facing and south facing slope of the rock outcrop.
<i>Usnea aurantiaco - atra</i> (Jacq.) Bory.	Fruticose thallus. Collected for laboratory studies only from a north facing slope at Woozle Hill, Galindez Island.

lower surface projection and the surface of the sides of the hypothetical cylinder (in case of a flat thallus the height of the cylinder was the thickness of the thallus). For *Umbilicaria propagulifera* the lower surface area was multiplied by two, an estimate for the surface increase due to the rhizoids and based on microscopical investigations. Five to ten measurements on randomly chosen cross sections of water-saturated thalli were made, the mean being used as an estimate of thallus thickness.

Results

Field observations

Data on the water content of the thalli in the field during the four day period are given together with the relative humidity and the periods of precipitation in Fig. 1. Mean wind speed during the observation period was high (12 m s^{-1}), gradually declining to 1 m s^{-1} at the end of the wet period, after which the wind speed increased again to 12 m s^{-1} by the end of the observation period.

Initially the lichen thalli were relatively dry, with moisture

contents mostly between 20–25% of dry weight. Just after 14h00 on 13 February light rain began, and the water content of all species increased rapidly, until saturation seemed to be reached at 18h00. 14 and 15 February were days with nearly continuous light rain, sleet or snow. Regular two-hourly observations were resumed on 16 February, a dry, but mostly overcast day. With a cessation of precipitation, the thalli dried out within a few hours (Fig. 1). Maximum water contents were highest in *Mastodia tessellata* from the shoreline and lowest in *Usnea antarctica*. *Usnea antarctica* from the north face of the outcrop showed a more rapid fluctuation in water content than thalli collected from the south facing slope. Rates of water loss and uptake in *M. tessellata* were approximately twice as high in the shoreline population as in the more inland population. Minimum water contents of thalli during the observation period varied between 15% (*Pseudophebe pubescens*) and 52% (*M. tessellata*).

Laboratory studies

The water loss of saturated lichen thalli during 12 hours of exposure to a desiccating atmosphere is shown in Fig. 2. The

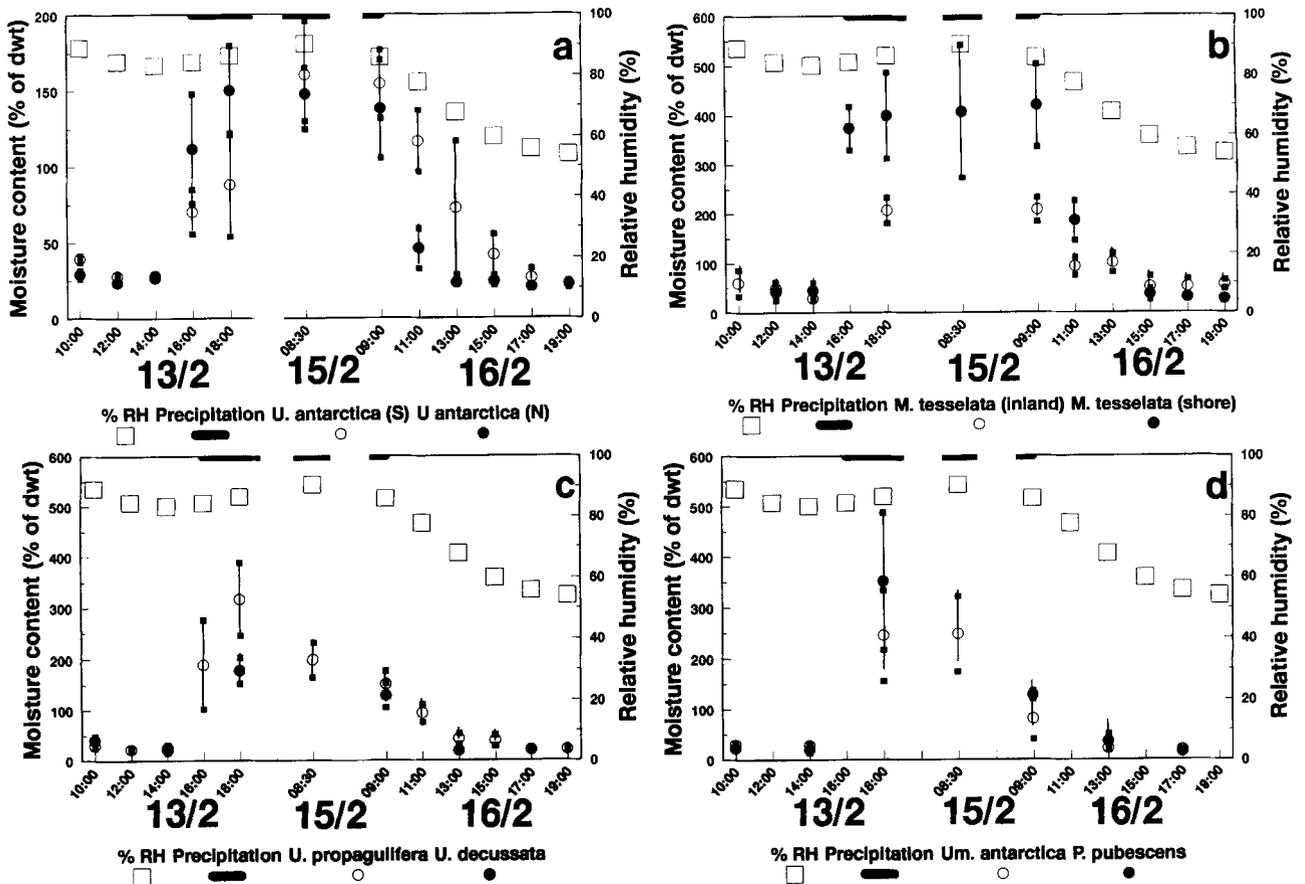


Fig. 1. Moisture content (in % of dry weight) of thallus samples of different lichen species collected at different times from the rock outcrop. The symbols represent the mean of five samples; the vertical bars represent two standard errors and give the 95% confidence interval of the mean. % RH measured at the meteorological observatory.

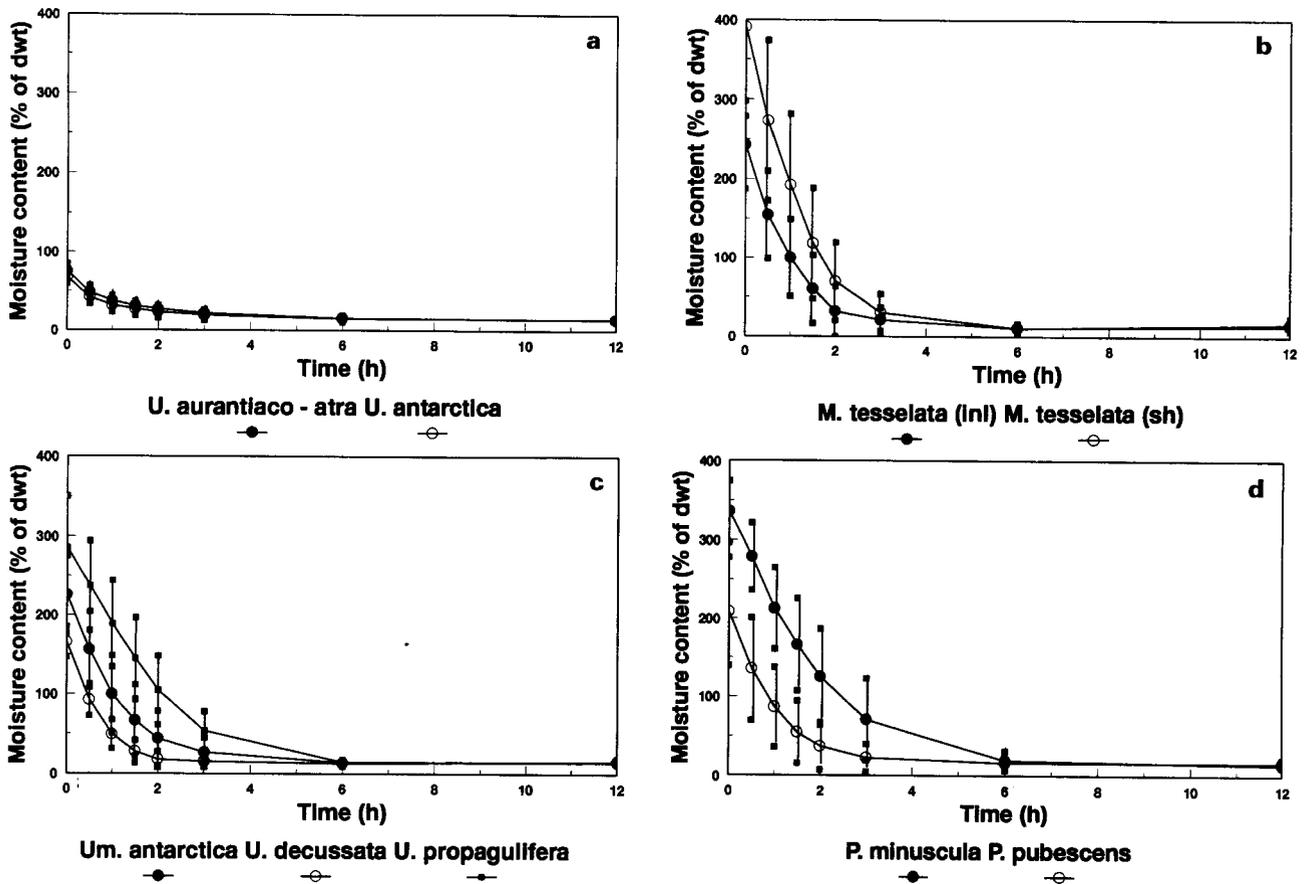


Fig. 2. Water loss of lichen thalli (averages of 15–20 thalli) under laboratory circumstances during exposure to a desiccating atmosphere. The vertical bars indicate two standard errors and give the 95% confidence intervals of the mean values.

initial water content of the lichen thalli, assumed to be their saturation water content, varied considerably between the species: from *c.* 67% in *Usnea antarctica* to almost 400% in the shore samples of *Mastodia tessellata*.

Some species dried out rapidly, notably *M. tessellata*, *Umbilicaria decussata* and *Pseudephebe pubescens*, reaching equilibrium with the atmosphere in 2–3 h. All species reached an equilibrium water content in *c.* 6 h. The equilibrium water content of 14–16% was similar for all species. Initial water loss was highest in *U. decussata* (over 70% of the initial water content was lost in the first hour), and lowest in *U. propagulifera* and *Pseudephebe minuscula* (34% and 37%). The other species lost *c.* 50% of their initial moisture content during the first hour.

The desiccation experiment had to be undertaken as two experiments for reasons of space. The first used both *Usnea* species and both *Pseudephebe* species were studied whilst the *Umbilicaria* species and the two populations of *M. tessellata* were measured in the second experiment. Temperature and RH for the two experiments were sufficiently different to limit a statistical comparison of the species to each experiment. The results of the significance tests, using a repeated measures ANOVA showed significant differences

in the desiccation between all pairs of species ($P < 0.01$) except that the difference between the curves of *Usnea antarctica* and of *U. aurantiaco-atra* was only just significant ($P = 0.03$).

Water uptake by lichen thalli during the first 24 h of exposure to the saturated atmosphere ranged from 18% (for *Pseudephebe minuscula*) to 26% (for *Umbilicaria antarctica*). Rates of water uptake decreased with time and the thalli had not regained their saturated water content even after 160 h.

The relation between surface area to volume ratio and water uptake and loss is shown in Table II. The table is arranged in descending order of surface/volume ratio. As the water uptake and loss rates followed in most cases an exponential function, the water contents were converted into logarithmic values. In Table II water uptake and loss rates are shown over the complete uptake and desiccation period. All species show higher water loss rates in the laboratory experiment as compared to those determined in the field study, except for the water loss rate of *Usnea antarctica* from the north face of the rock which is higher than the water loss rate in the field. The rates of water uptake in the field are all higher than the loss rates. *Pseudephebe minuscula* has the highest surface/volume ratio and shows an average water loss

Table II. Ratio of surface area to volume, moisture uptake and loss rates in the field and loss rates in the laboratory experiment for the lichen species studied. Experimental data expressed as natural logarithms of rate per hour.

Species (habitat)	surface/volume ratio	field expt. moisture uptake	field expt. moisture loss	lab expt. moisture loss
<i>Pseudephebe minuscula</i>	33.4			0.53
<i>Pseudephebe pubescens</i>	26.7	0.79	0.27	0.86
<i>Mastodia tessellata</i> (inland)	25.8	0.31	0.21	0.47
<i>Mastodia tessellata</i> (shore)	20.8	0.56	0.37	0.53
<i>Usnea aurantiaco - atra</i>	20.1			0.28
<i>Usnea antarctica</i> (N)		0.40	0.39	
	14.3			0.26
<i>Usnea antarctica</i> (S)		0.46	0.19	
<i>Umbilicaria propagulifera</i>	13.8	0.69	0.25	0.50
<i>Umbilicaria antarctica</i>	11.8	0.57	0.35	0.46
<i>Umbilicaria decussata</i>	5.3	0.55	0.47	0.78

rate in the laboratory experiment. *P. pubescens*, with a lower, but still comparatively high surface/volume ratio, has a relatively high uptake rate in the field experiment, a relatively low loss rate in the field experiment, and a relatively high loss rate in the laboratory experiment. A comparison of the *Umbilicaria* species shows that *U. decussata* with the lowest surface – volume ratio shows relatively high uptake and loss rates in the field and a high loss rate in the laboratory experiment. The other *Umbilicaria* species show a higher uptake rate of water in the field study when the surface to volume ratio is higher, the loss rates in the field show an opposite reaction. The *Usnea* species show relatively low loss rates in the laboratory. Under field circumstances differences in uptake and loss rate were found for the north and south facing slope.

The samples from the two *Mastodia* populations showed differences, both in surface/volume ratio as well as in uptake and water loss rates. In the inland population with the higher surface/volume ratio lower uptake – and loss rates were found.

Discussion

With one exception maximum and equilibrium water contents in this study agree with data presented by R.I.L. Smith (1988) and Sancho & Kappen (1989) (Table III). However the maximum water content of 260% reported by Sancho & Kappen (1989) for *Umbilicaria decussata* is about twice the value found in this study and by R.I.L. Smith (1988). We have no explanation for this difference.

In the field there was a rapid response of thallus water content to changes in water availability in the lichen's environment. Although water uptake and loss is largely synchronous between species, and likely to be governed by the microclimatic circumstances, the rates at which this occurs differ widely. These rates have been shown to be strongly dependent on the morphology and size of the thallus

Table III. Minimum and maximum thallus water content figures reported in the literature. Sources are: ¹RIL Smith 1988, ²Sancho & Kappen 1989, ³Kappen 1985a, ⁴Kappen 1985b.

	laboratory		field	
	maximum	minimum	maximum	minimum
<i>Pseudephebe minuscula</i>	350 ¹	12 ¹	340 ¹	11 ¹
<i>Umbilicaria decussata</i>	130 ¹	14 ¹	140 ¹	12 ¹
	260 ²	18 ²	151 ³	
<i>Usnea antarctica</i>	85 ¹	15 ¹		
<i>Usnea aurantiaco - atra</i>			164 ⁴	

(Larson & Kershaw 1976, Larson 1979, 1981, 1984, Rundel 1982, Lange & Kilian 1985). Larson (1981) found an increase in water uptake rate with increasing surface to weight ratio in 11 species of lichens using microscopic glass beads adhering to the moist thallus surface to determine the surface area of the thallus. Snelgar & Green (1981) and Rodgers (1976) found similar relationships, but within a collection of thalli from a single species. Our results show for *Pseudephebe pubescens*, with a relatively high surface to volume ratio, a relatively high rate of moisture uptake rate and a relatively low rate of moisture loss under field circumstances. For *Umbilicaria antarctica* and *U. propagulifera* with lower surface to volume ratios uptake rates were relatively lower and loss rates were higher. These species follow the expected trends between surface to volume ratios and water relations. *U. decussata*, with the lowest surface to volume rate and an uptake rate similar to that of *U. antarctica* but with a higher moisture loss rate in the field, does not. Thalli of *Usnea antarctica* collected from the south facing slope showed higher uptake rates and lower loss rates as compared to thalli collected from the north facing slope, although their surface to volume ratio was similar. This difference can only be ascribed to the differences in water availability on both slopes, the north facing slope being the more exposed.

We found significant differences between thalli of *Mastodia tessellata*. Despite the differences in morphology of the thalli of the two populations they, nevertheless, belonged to the species *M. tessellata* (D.O. Øvstedal, personal communication). Thalli exposed to sea water contained 200–400 mmol Cl⁻ kg⁻¹ while thalli from the more inland population contained only 2–4 mmol Cl⁻ kg⁻¹. The thalli with the higher salt content showed a rapid uptake of water probably because of the hygroscopic nature of the salt, and a retarded moisture loss (as shown in the laboratory experiment Fig. 1b). The higher water loss rate in the field in comparison with the water loss rate in the inland population, might be due to the rain washing out most of the salt, resulting in a higher water loss rate which was more in agreement with the differences in surface/volume ratio of the thalli of both populations. Maximum field moisture content of the thalli from the shore population was twice that of the thalli from the rock outcrop. These findings agree with the results presented by Follmann (1967) and Nash III *et al.* (1979) describing the

hygroscopic action of salt in thalli from the sea shore.

For most species the maximum water content found in the field is similar to that found in the laboratory experiments (cf. Figs 1 & 2). Exceptions are *P. pubescens* and *Usnea antarctica*, where maximum field water contents are c. 50% and 100% higher than those attained under laboratory conditions. These maximum field water contents were observed during rain. In the foliose *Umbilicaria* and *Mastodia* presumably the light shaking given to the thalli upon collection was sufficient to remove rain or melting snow. In the fruticose *Usnea antarctica* and *P. pubescens* it is possible that not all external water was removed.

The lower relative humidity of the air in the laboratory experiment probably accounts for the higher minimum water contents measured in the field and the higher rates of water loss in the laboratory experiments.

Water uptake in our laboratory experiments was low, much lower than rates reported by Lange *et al.* (1970) and others (e.g. Kappen 1980, Larson 1981, Kappen 1985b, Kershaw 1985, Lange *et al.* 1994). In our experiment the lichen thalli were exposed to humid air only. Spraying of the thalli (Kappen *et al.* 1980, Larson 1981, Kappen 1985b) resulted in a much faster uptake of water. Uptake of water from humid or foggy air can be an extremely slow process exceeding 50 h (Lange & Kilian 1985). Compared with these results, the slow uptake of water in the laboratory experiment is not exceptional.

This paper shows that although the microclimate may be the driving force for the water relations in lichens morphological and anatomical differences between thalli may result in distinctly different uptake and loss rates of water. Fruticose and foliose lichen species collected from the same habitat, a north-exposed rock outcrop, showed strong variation in their water uptake and water loss, in the field as well in the laboratory. Rates of uptake also depend on whether uptake is from liquid water or from a saturated atmosphere. With a similar microclimate, the surface to volume ratio of the thalli governed the water relations of the different species but there are still differences which cannot be explained from the findings in this study.

In general comparative studies under laboratory conditions support the same conclusions as the results obtained in field studies. However, comparing samples of a single species (*Usnea antarctica*) from the exposed north slope and the more sheltered south slope showed the strong influence of the local microclimate on thalli of similar surface to volume ratio, a result that was not clear in the laboratory studies.

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