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2.5 Aspects of Cryptogam Water Relations at a Continental Antarctic Site

By Ronald I. Lewis Smith*

Summary: The loss of water in a desiccating atmosphere (c. 40% r. h. at 10° C) and uptake of water from a saturated atmosphere (100% r. h. at 10° C) was recorded at intervals over periods of many hours or days in the dominant mosses and macrolichens occurring near the Australian Casey Station. Wilkes Land, continental Antarctica. While major differences exist in the water holding capacity and rates of water loss between mosses and lichens, the minimum levels attained after prolonged exposure to desiccating conditions are remarkably similar. By contrast, the volume of water absorbed from a saturated atmosphere is very similar in both groups of cryptogams. Morphological and anatomical characters are responsible for many of the differences, both between species, and within species exhibiting different growth features. Thus, significantly larger amounts of water are held by colonies of *Bryum algens* with a dense tomentum of rhizoids than those with sparse rhizoids; similarly, the rhizinate *Umbilicaria aprina* held a greater volume of water than the erhizinate *U. decussata*. The filamentous mat form of *Alectoria minuscula* permits a much higher water content to be attained than in the coarser fruticose forms of *Usnea sphacelata* and *U. antarctica*. The dense shoot arrangement in *Schistidium antarcticum* accounts for the high water holding capacity in the hydric turf form whereas the less densely packed shoots and thicker cell walls of the xeric cushion form maintain a lower water content. The rate of water loss (as percentage dry weight) was much faster in the turf form of *Schistidium* and tomentose form of *Bryum*, although this trend was reversed when expressed as percentage of the intitial water content. Minimal water contents are achieved by the lichens in desiccating conditions within 6—12 hours, whereas the mosses take several times longer. The water relations characteristics of these cryptogams are considered in the light of their distribution in the field and of their metabolic activity under prevailing Antarctic conditions.

Zusammenfassung: Bei den nahe der australischen Station Casey, Wilkes Land, in der kontinentalen Antarktis am häufigsten vorkommenden Moosen und Markolichenen wurden der Wasserverlust unter austrocknenden Bedingungen (ca. 40% bei 10° C) udn die Wasseraufnahme utner wassergesättigten Bedingungen (100% bei 10° C) bestimmt. Während sich große Unterschiede im Wasserhaltevermögen und im Wasserverlust zwischen Moosen und Flechten ergaben, waren nach einer langen Austrocknungsperiode die Minima bemerkenswert ähnlich. Im Gegensatz dazu war die Wasseraufnahme bei wassergesättigten Bedingungen in beiden Kryptogamengruppen gleich. Morphologische und anatomische Eigenschaften sind für viele der Unterschiede verantwortlich. Dies gilt für den inter- und auch den intraspezifischen Vergleich, wobei unterschiedliche Wuchsformen eine wesentliche Rolle spielen. Polster von *Bryum algens* mit dichtem Rhizoidfilz können größere Wassermengen halten als solche mit lockerem Rhizoidbesatz. Gleichermaßen ist bei der rhizinientragenden *Umbilicaria aprina* das Wasserhaltevermögen größer als bei *U. decussata*, die keine Rhizinien besitzt. Die feinfädigen Matten von *Alectoria minuscule* erreichen einen höheren Wassergehalt als die gröber strukturierten Formen von *Usnea sphacelata* und *U. antarctica*. Bei *Schistidium antarcticum* führt das dichte Zusammenliegen der Sprosse in den hygrophytischen Polstern zu einem höheren Wasserhaltevermögen, während die xerophytischen Kissen mit ihrer lockeren Sproßanordnung und den dickeren Zellwänden nur einen niedrigeren Wassergehalt erreichen. Bezogen auf das Trockengewicht erscheint die Kurve des Wasserverlustes bei der Polsterform von *Schistidium* und der tomentosen Form von *Bryum* wesentlich steiler als diejenige bezogen auf 100% des Ausgangsgewichtes. Beim Austrocknen erreichten Flechten minimale Wassergehalte nach 6—12 Stunden, während Moose ein vielfaches dieser Zeit benötigen. Die Wasserhaushaltstypen dieser Kryptogamen werden im Hinblick auf ihre Verbreitung am natürlichen Standort und ihre Stoffwechselaktivität unter antarktischen Bedingungen diskutiert.

1. INTRODUCTION

The occurrence, distribution pattern and association of plants in the Antarctic is dependent to a large extent on the presence of liquid water, at least intermittently, during the summer. Bryophytes and lichens comprise the great majority of the macrophytes of the Antarctic biome and the existence of many species and the assemblages they create are determined to a large degree by the moisture regime of the substratum or, to a lesser extent, by the relative humidity regime of the atmosphere. Both factors are themselves controlled by the climatic conditions prevailing in a region and, in continental Antarctica, these become increasingly critical as the climate becomes colder, drier and windier. The vegetation of the maritime Antarctic is relatively diverse and stands are often continuous over extensive areas of summer snow-free lowland terrain where there is frequent rainfall and widespread snow melt in summer (GIMINGHAM & SMITH 1970; SMITH 1972, 1984; LONGTON 1985). In coastal continental Antarctic regions summer precipitation is generally low and falls as snow. Surface temperatures are sufficiently high to allow considerable melting of this and winter snow, and water is available for varying periods throughout the short summers, allowing localised extensive stands of vegetation to develop (LONGTON 1973, 1979, SEPPELT & ASHTON 1978, KAPPEN 1985a, KANDA 1987). However, in inland and coastal ablation areas, precipitation and temperatures are usually so low that free water is rarely available except along melt channels; here, too, relative humidity can be exceedingly low for very long periods. Thus, inland continental sites have a very restricted flora which rarely develops stands of any significant size (e. g. SIPLE 1938, PICKARD 1986, ENGELSKJØN 1987, HALE 1987) and individual plants (chiefly lichens) maintain their presence almost entirely by absorption of atmospheric moisture.

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It is widely acknowledged that habitat selection and geographical distribution of bryophytes and lichens is governed largely by the water requirements of individual species in relation to their anatomy and morphology (e. g. LARSON 1981, LONGTON 1988). This has been extensively reviewed for broyphytes by PROCTOR (1982, 1984) and for lichens by BLUM (1973) and HARRIS (1976). However, very few studies have been made of the water relations of Antarctic cryptogams, although these are crucial to the metabolic activity of these plants in such a physiologically stressful environment and, consequently, of the ecological relationships of the vegetation. Thus GIMINGHAM & SMITH (1971) interpreted the ecology of maritime Antarctic mosses in terms of the relationship between growth form and water balance, while KANDA (1986) reported changes in the water content in moss communities throughout a summer at a coastal continental site. LANGE & KILIAN (1985), KAPPEN (1985b, c) and KAPPEN & REDON (1987) examined the photosynthetic rate of Antarctic lichens in response to their water relations.

The present study was undertaken in collaboration with the Australian Antarctic Division at Casey Station, Budd Coast, Wilkes Land, coastal continental Antarctica. It was part of an investigation of the structure and dynamics of the cryptogam communities of Bailey and Clark Peninsulas, and of the importance of temperature and water in the micro-distribution of the principal plant species (SMITH 1986, 1988 a, b). This study examines, somewhat simplistically, because of inadequate equipment and laboratory facilities, the atmospheric water relations, in terms of rates and volumes of water loss and uptake, of most of the region's dominant mosses and macrolichens. It developed out of the study of species distributions along environmental gradients (SMITH, in press). However, the data obtained helped to characterise the ecological and physiological behaviour of the plants and provide relevant background information for the intensive study of photosynthesis and respiration in these plants carried out by L. Kappen and his co-workers during the same field period.

Avascular cryptogams possess few specialised mechanisms for water conservation, relying primarily on morphological or growth-form features such as dense packing of shoots, sinuous twisting of leaves during dehydration or a dense arrangement of rhizoids or rhizinae, or anatomical features such as wax deposits on moss leaves and thickening of the outer cortex in lichens, thickened cell walls and bistratose cell arrangements in mosses, and air spaces and changes in the proportion of algal to fungal cells in lichen thalli. However, these serve only to reduce the rate of water loss since mosses and lichens are renowned for their ability to withstand long periods of excessive desiccation at both high and low temperatures, yet resume normal metabolic rates on rehydration. While a resumption of the hydrated state is generally achieved by capillary uptake of liquid water from the substrate or by absorption of water directly from precipitation, these plants can also maintain tissue moisture contents adequate for their physiological processes merely by the absorption of moisture from a humid atmosphere. With a few exceptions, water uptake and loss by bryophytes and lichens are largely uncontrolled passive, rather than active, processes (LONGTON 1988).

2. MATERIAL

All three moss species occurring in the Casey area have wide ecological amplitudes. In particular the non-rhizoidal *Schistidium antarcticum* (Card.) Savicz et Smirn. (=*Grimmia antarctici* Card.) ranges from closed, extensive mesic or hydric turves of densely packed and abundantly branched shoots with thin-walled cells in wetter habitats, to small but less densely packed almost spherical xeric cushions on dry windswept substrata; in this form leaf cells have significantly thicker walls. *Bryum algens* Card. (= *B. pseudotriquetrum* (Hedw.) Schwaegr.) occupies a similar range of habitats but forms closed stands over very small areas in moist situations. However, individual shoots vary from those possessing only sparse rhizoids to those with a dense tomentum. During dehydration the leaves twist and adhere tightly against the stem.

The dominant fruticose lichen *Usnea sphacelata* R. Br. (= *Usnea sulphurea* (Koenig) Th. Fr.) is a lithophyte with a bushy thallus attached to the rock by a holdfast on the central stem. It develops a progressively thicker cortex with increasing exposure to wind. Growth-form ranges from robust, almost "woody" but sparsely branched black plants in windswept situations to slender finely but densely branched grey plants in sheltered habitats. Where extreme shading and shelter occur the thalli may comprise only a few long yellow filamentous branches. *Usnea antarctica* Du Rietz is similar but grows predominantly in sheltered habitats and often epiphytically on the moss *Ceratodon purpureus* (Hedw.) Brid. *Alectoria minuscula* (Nyl. ex Arnold) Degel (= *Pseudephebe minuscula* (Nyl.

ex Arnold) Brodo & Hawksw. grows as compact prostrate dense black mats of fine intertwined branches on rock. The two foliose species *Umbilicaria aprina* Nyl. and *U. decussata* (Vill.) Zahlbr. form disc-like thalli of up to several centimetres across and attached to rock by a central short holdfast. In small plants the abaxial surface of the thallus is always in close contact with the substratum but, during desiccation events, the margins of larger plants rise up as the thallus dehydrates and contracts. The underside of *U. decussata* is plain (erhizinate), while that of *U. aprina* has dense patches of rhizines. In *U. decussata* the upper surface is rugose and reticulated which may facilitate rapid uptake of atmospheric moisture by increasing the surface area.

3. METHODS

3.1 *Water Loss in a Desiccating Atmosphere*

For the water loss experiments freshly collected plant material was returned to the laboratory and individual lichen thalli or moss colonies placed on several layers of tissue paper saturated, but not flooded, with deionised water. This treatment was carried out in a small polystyrene container which was then sealed and left for 12 hours, permitting the samples to become fully hydrated. Before water loss was monitored any extraneous water was removed by lightly blotting the samples with tissue paper. The sides and base of the moss turf cores and the base of the entire moss cussions were sealed with non-porous tape to restrict water loss to the apices of the stems. In each experiment from 10 to 20 replicate samples per species were weighed then suspended by fine wire in an atmosphere maintained as constantly as possible at 10° C and in a relative humidity of 40%, i. e. conditions which promote relatively rapid evaporation but which are commonly encountered at the substrate-atmosphere interface in the field on calm, overcast days. Water loss was recorded by reweighing each replicate initially at 10 or 15 minute intervals over the first 1—2 hours, then half-hourly over the next two hours, hourly over the next 2—3 hours and subsequently at 12 hourly intervals. At the end of each experiment the oven-dry weight of each sample was obatined. A computer programme was written to convert the data to water loss as a percentage of the dry weight and also as a percentage of the initial sample water content, and to generate decay curves of the averaged data.

3.2 *Water Uptake from a Saturated Atmosphere*

Samples identical to those used in the water loss trials were exposed to a warm desiccating atmosphere for several days to reduce the lichen thallus or moss shoot water content to a minimum (approximately 10—20% of the dry weight). This remaining water is the "bound water" fraction contained within the cells and which requires considerable heat to completely dehydrate the tissues. Ten to 20 replicates per species were then suspended in a sealed wide-necked 2 l conical flask containing 250 ml of deionised water which maintained a saturated atmosphere (checked at 12-hourly intervals). Most sets of samples were reweighed after 12 and 24 hours, although one series of moss samples was reweighed at 12 hourly intervals over 12 days. For all samples oven-dry weights were obtained at the end of each experiment and the data calculated as water content expressed as a percentage of the dry weight.

4. RESULTS

4.1 *Water Loss*

The water loss decay curves for each species are illustrated in Figures 1—6. The data points are not given since the curves fitted almost perfectly through all points. Standard errors of the mean of each point are also not shown since these were invariably small, ranging from 4—8% of the highest mean water contents (e. g. 350—700% of the dry weight) to 1—5% for the lowest (e. g. around 12—20% dry weight) (see Table 1). The water holding capacity (i. e. the initial water content at full hydration) of the two growth forms of *Schistidium* was significantly different, the turf form (cut to 1 cm tall) holding four times that of the cushion form (*c.* 1 cm tall) (Fig. 1). This was clearly related to shoot density (i. e. the number of apices reaching the surface of the colony). Mean values for three moist samples of each form were 1480 ± 329 shoots cm^{-2} in the mesic turf and 640 ± 186 shoots cm^{-2} in the xeric cushion. Water loss from the apices only of these colonies on a dry weight basis was considerably slower in the cushion form, yet reached virtually identical water retention capacity (i. e. the final moisture content at minimal hydration) after six days. However, when expressed as a percentage of the initial water content the cushion form exhibited the faster rate. In short samples of *Schistidium* turf (*c.* 0.5 cm), from which water loss was

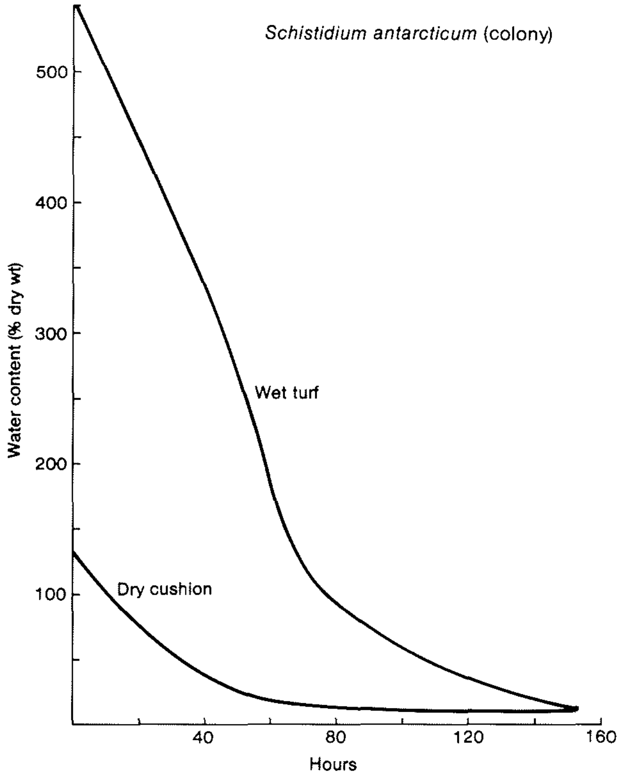

Fig. 1: Water loss (as percentage dry weight) in two growth forms of *Schistidium antarcticum*.

	Time (hr)				
Species and growth form	0	1	6	12	24
Schistidium antarcticum					
(entire cushion)	(133±18)	2	16	33	51(65±13)
(tall turf)	(554±31)	1	6	15	23(425±27)
(short turf)	(565±14)	7	26	40	70(170± 6)
Bryum algens					
(short turf, dense rhizoids)	(717±30)	8	29	44	72(198±18)
(short turf, sparse rhizoids)	(182±15)	16	44	59	73(51± 4)
Usnea sphacelata					
(robust form)	(73± 4)	36	70	75	78(16± 1)
(fine form)	(114± 8)	53	86	87	87(15±0.2)
(shade form)	(103± 3)	42	79	85	85(16±0.2)
Usnea antarctica					
(robust form)	(85± 6)	52	81	82	82(15± 3)
(fine form)	(83± 2)	42	81	82	82(15±0.4)
Alectoria minuscula	(351±20)	23	83	97	97(12±0.4)
Umbilicaria decussata	(130± 3)	48	86	88	89(14±0.7)
Umbilicaria aprina	(204±11)	34	88	94	94(12±0.1)

Tab. 1: Mean water loss by mosses and lichens at 40% R.H., 10° C (%initial water content). Values in brackets are water content (%dry wt) ± one standard error of mean (n = 10–20).

also confined to the apices only, the initial and final water contents were almost identical to those of the taller turves, but the minimum water content was achieved in a much shorter time (Fig. 2). The two forms of *Bryum algens* (both *c.* 1 cm tall) showed significant differences in behaviour, those samples with dense rhizoids holding four times more water than those with sparse rhizoids (Fig. 2). Clearly the tomentum serves an important role as a reservoir of water. The respective rates of loss were similar to those found in the hydric and xeric forms of *Schistidium*.

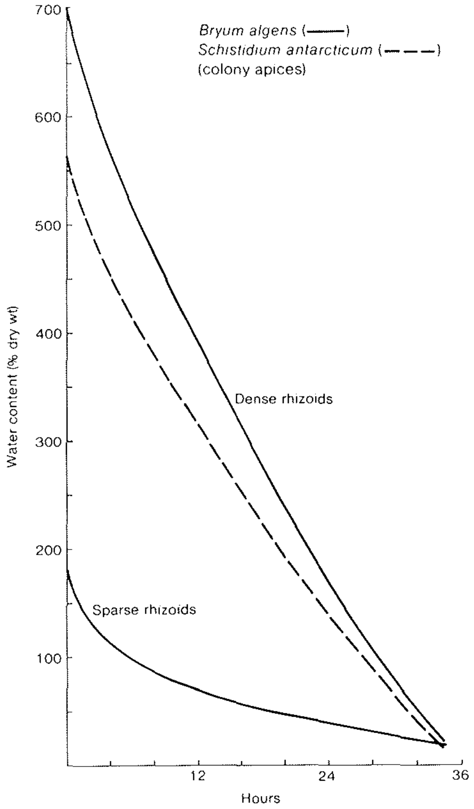

Fig. 2: Water loss (as percentage dry weight) in short turf colonies of *Schistidium antarcticum* and *Bryum algens* (with dense and sparse rhizoids).

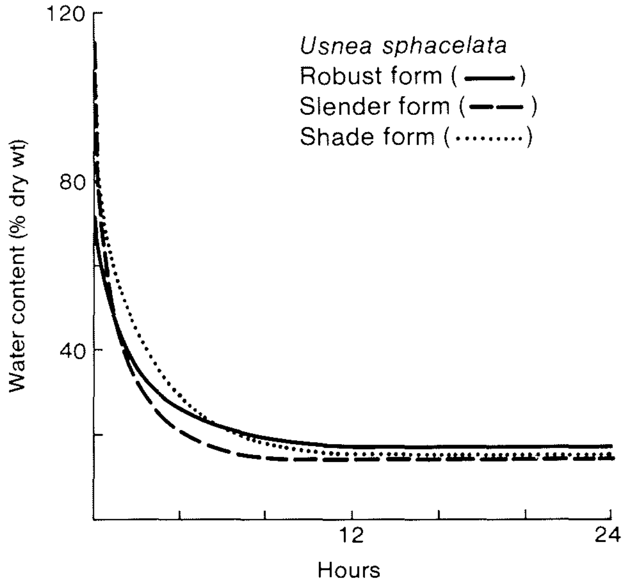

Fig. 3: Water loss (as percentage dry weight) in three growth forms of *Usnea sphacelata*.

Water loss in *Usnea sphacelata* was extremely rapid and all three growth forms followed almost identical decay rates (Fig. 3). However, the thickly corticated robust form had a water holding capacity considerably less than that of the finely branched forms with thin cortices, but all reached almost the same water retention capacity after only about 8 hours. As with the two dominant forms of *Usnea sphacelata*, the pattern of water loss in the two

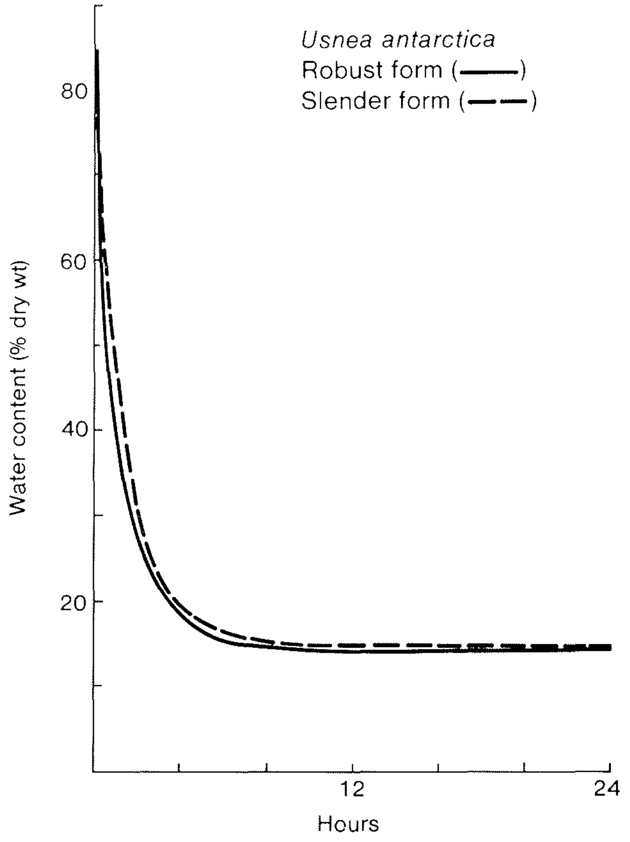

Fig. 4: Water loss (as percentage dry weight) in two growth forms of *Usnea antarctica*.

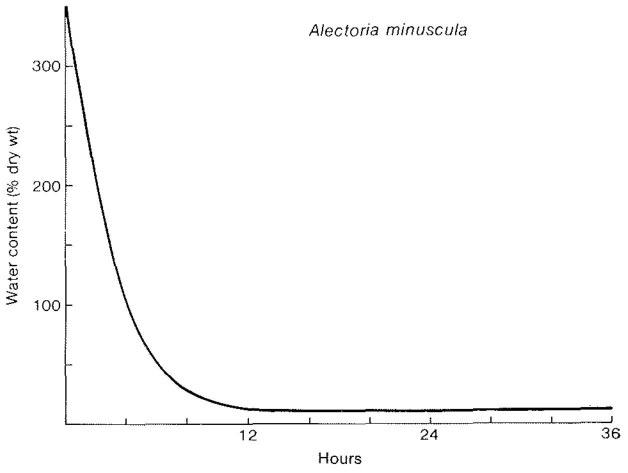

Fig. 5: Water loss (as percentage dry weight) in *Alectoria minuscula*.

forms of *Usnea antarctica* was virtually identical (Fig. 4). However, their initial water holding capacity was less than in *U. sphacelata* and minimal water content was achieved after only about 6 hours. The larger but more sparsely and thicker branched epiphytic form holds a greater volume of water, but this form was not examined here. The interwoven filamentous mats of *Alectoria minuscula* exhibited quite a rapid rate of loss from a high initial water holding capacity irrespective of thallus size, but reaching a minimum level similar to that in the Usneas (Fig. 5). In the foliose Umbilicarias, the rhizinate *U. aprina* had a considerably higher water holding capacity than the erhizinate *U. decussata*. However, both lost water at comparable high rates to achieve virtually the same low water retention capacity (Fig. 6).

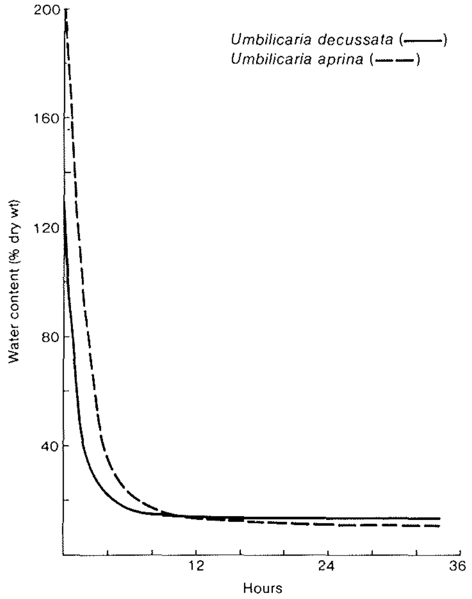

Fig. 6: Water loss (as percentage dry weight) in *Umbilicaria decussata* and *U. aprina*.

In a field experiment in situ thalli of *Usnea sphacelata* and *Umbilicaria decussata*, lightly sprayed with deionised water 10 minutes before sampling commenced, had initial and final water contents almost identical to respective samples in the laboratory experiments, but the rates of loss were more rapid (Fig. 7). This was accounted for by the plants being exposed to direct sunshine which raised thallus temperatures considerably, thereby increasing the rate of evaporation. However, adjacent *Usnea* thalli in slight shade continued to take up superficial moisture for half an hour after spraying but then inexplicably lost water even more quickly than the unshaded plants.

Data from the water loss decay curves are compared (Tab. 1) over the first 24 hours in each experiment. The initial and final water content (as percentage dry weight) is given at time 0 and after 24 hours, respectively, and as a percentage of the inital water content after 1, 6, 12 and 24 hours. The data clearly illustrate the great difference in rate of loss (as percentage of initial water content), irrespective of the initial water holding capacity (as percentage dry weight), between the mosses and lichens. For example, after 1 hour less than 16% of the initial volume of water had been lost by the mosses while about 30—50% was lost by the lichens; after 12 hours the losses were still mostly less than about 50% in the mosses but over 80% in the lichens. The approximate times taken by each species to achieve maximum water loss are compared in Table 2.

4.2 *Water Uptake*

In contrast to water loss, the rate and volume of uptake of atmospheric moisture under controlled conditions is remarkably similar in both the aggregations of moss shoots and in lichen thalli (Tab. 3). In most species maximum uptake is achieved after about 12 hours exposure in a saturated atmosphere, with water contents (as percentage dry weight) after 24 hours ranging from 43% in *Usnea sphacelata* to 61% in *Bryum algens*. While increasing fineness of branches in *U. sphacelata* promotes progressively greater uptake, this is not exhibited by comparable

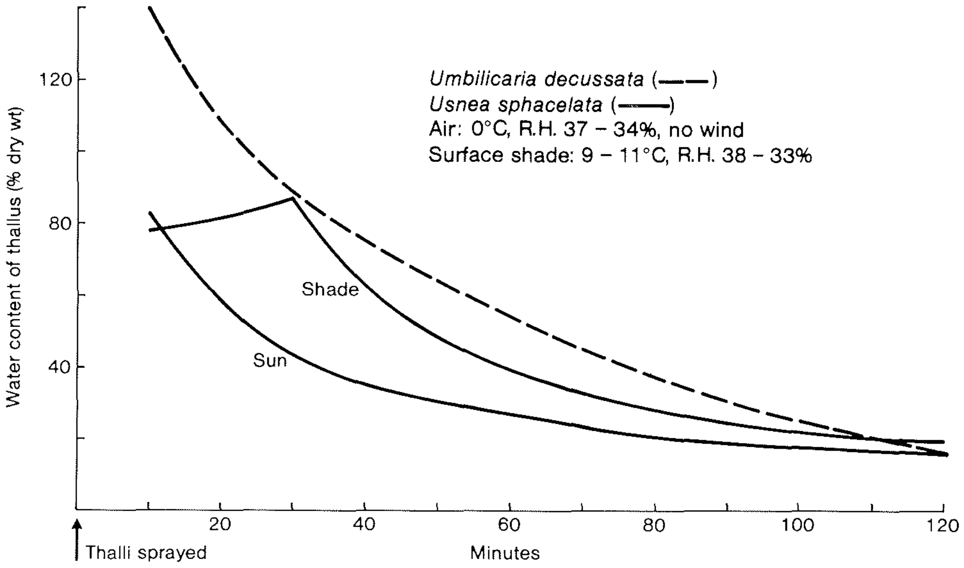

Fig. 7: Water loss (as percentage dry weight) in *Umbilicaria decussata* and *Usnea sphacelata* in situ, midday 17 December 1985.

Species and growth form	Mean approx. equilibration time (hr)
Schistidium antarcticum	
(entire cushion)	72
(tall turf)	150
(short turf)	36
Bryum algens	
(short turf, dense rhizoids)	36
(shurt turf, sparse rhizoids)	36
Usnea sphacelata	
(robust form)	11
(fine form)	7
(shade form)	10
Usnea antarctica	
(robust form)	8
(fine form)	8
Alectoria minuscula	12
Umbilicaria decussata	7
Umbilicaria aprina	10

Tab. 2: Time taken by mosses and lichens to reach maximum water loss at 40% R.H., 10° C. n = 10–20

growth forms in *U. antarctica*. The rhizinae of *Umbilicaria aprina* do not appear to enhance uptake, whereas the convoluted upper surface of *U. decussata* is probably responsible for the greater absorption.

In the mosses, the greater volume of water taken up apically by *Bryum* than by *Schistidium* results mainly from the larger leaf and cell size, rather than by the unexposed sub-surface tomentum in the former species. Since no liquid water is involved here the storage potential of the tormentum is not realised. This pattern was maintained over a prolonged period (Fig. 8). Following two days' exposure to desiccating (40% r. h.) conditions, the colony water content of *Bryum* with dense rhizoids decreased from 717% dry wt to 25% then rose to 117% (16% of the original water content) after 12 days in a saturated atmosphere; in *Bryum* with sparse rhizoids the colony water content declined from 182% to 17% then rose to 102% (56% of the original water content). Comparable values for *Schistidium* were 566% falling to 17% and increasing to 81% (14% of the original), respectively.
However, a major difference was recorded in the performance of individual shoots of *Bryum algens* in which uptake was possible over the length of the stem (i. e. not by the apex only, as in the colony aggregation samples). In contrast to the relatively low uptake by tomentose short turf, single shoots with dense rhizoids absorbed (and adsorbed?) five times more water after 12 hours (Tab. 3). The rhizoids are thin-walled and offer a very large

Species and growth form	Time (hr) 0	 12	 24
Schistidium antarcticum			
(short turf, apices only)	17	41	48
Bryum algens			
(shurt turf, dense rhizoids, apices only)	22	54	61
(single shoots, dense rhizoids)	32	268	189
(single shoots, sparse rhizoids)	18	145	151
Usnea sphacelata			
(robust form)	13	35	43
(fine form)	12	40	45
(shade form)	12	46	55
Usnea antarctica			
(robust form)	12	50	59
(fine form)	15	50	58
Alectoria minuscula			
(large thalli)	16	58	60
(small thalli)	11	40	48
Umbilicaria decussata	8	38	52
Umbilicaria aprina	12	29	45

Tab. 3: Mean water uptake by mosses and lichens from saturated atmosphere at 10° C (% dry wt). n = 10–20

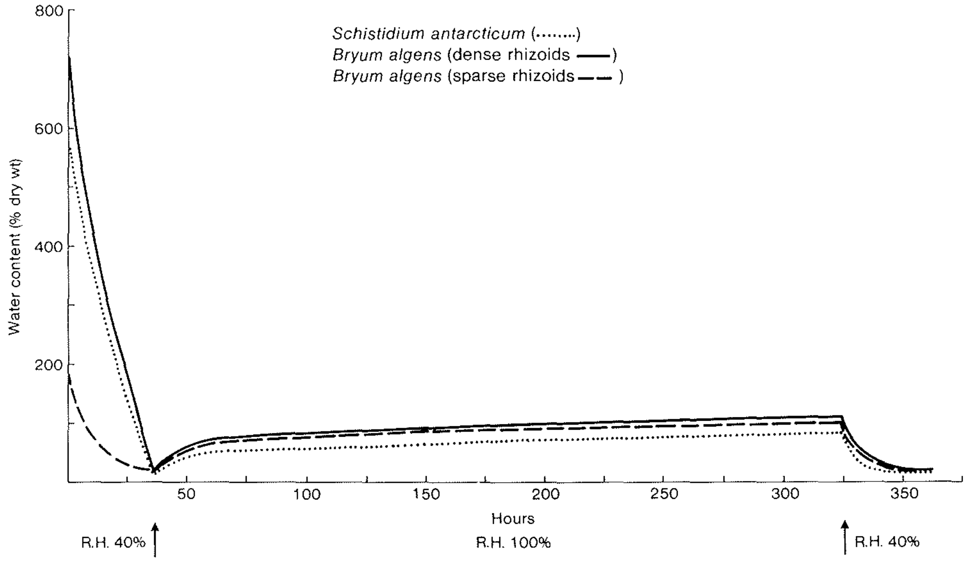

Fig. 8: Water loss in a desiccating atmosphere and uptake of water vapour from a saturated atmosphere in short turf colonies of *Schistidium antarcticum* and *Bryum algens*.

surface area which, if exposed to a humid atmosphere, are capable of talking up a substantial volume of moisture. The tomentum may have become super-saturated since there was subsequently loss of water over the next 12 hours. By contrast, in the shoots with sparse rhizoids the maximum water content achieved was considerably less after 12 hours but comparable after 24 hours. The tomentum plays an important role in the conservation of free water derived from a moist substratum or from precipitation and, by capillary action, provides the photosynthetically active apical leaves with water during desiccating conditions.

4.3 *Relationship between Water Holding Capacity and Plant Size*

The maximum thallus or colony water contents to plant size (in terms of dry weight) ratios for each species have been calculated from the initial data in each of the water loss experiments. To illustrate the trends within species all data points have been plotted (Fig. 9) and the ratios of the means and correlation coefficients are given in Table 4.

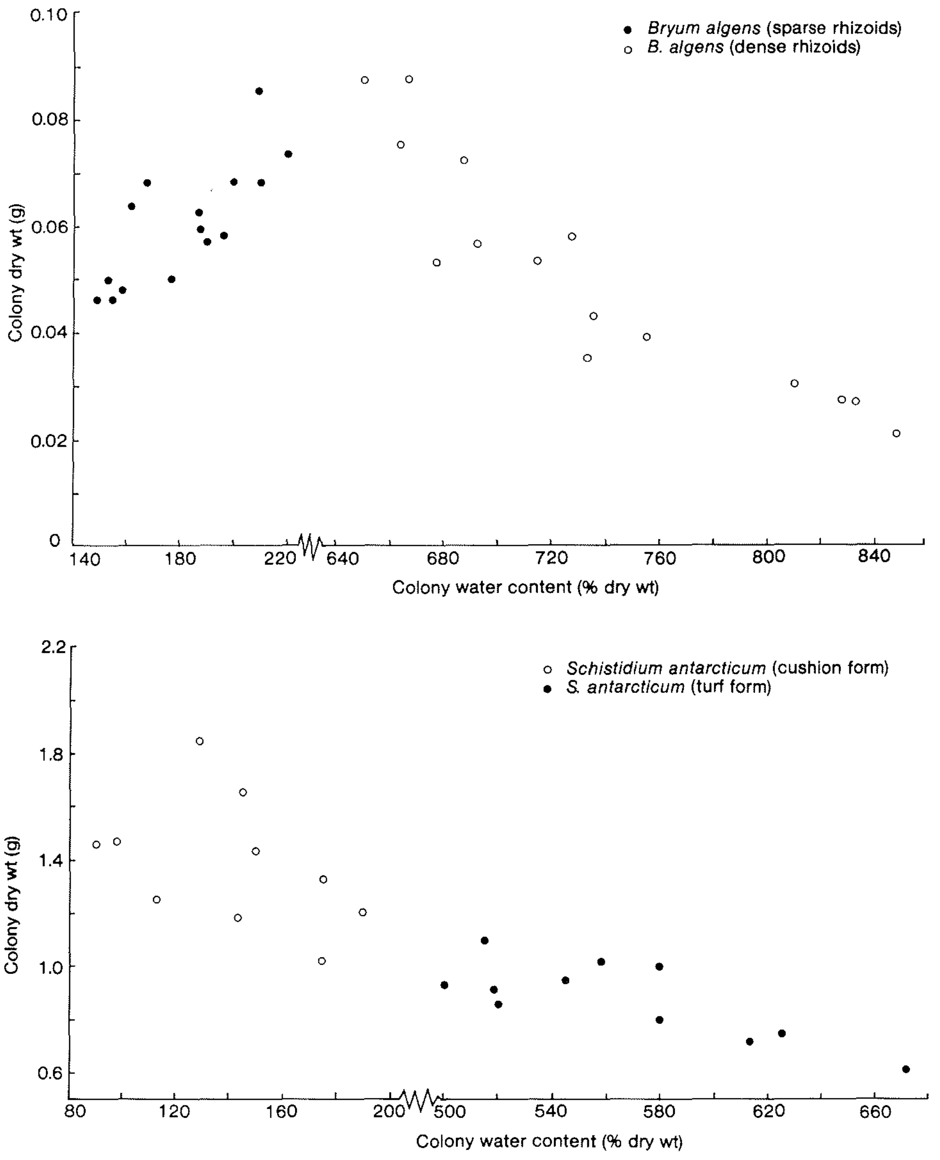

Fig. 9a: Relationship between maximum water holding capacity (as percentage dry weight) and sample dry weight in moss colonies.

The two forms of *Bryum algens* exhibit differing trends. Colonies with sparse rhizoids tend to hold more water as sample size increases, possibly as axillary water since there are generally more leaves present. Of all the species and growth forms examined, this was the only one which exhibited a positive correlation coefficient. However, in colonies with a dense tomentum, which occurs at the expense of leaves, the water holding capacity increases considerably as dry weight declines, giving a strong negative correlation. While individual rhizoids have a very small mass, collectively they may have a considerably greater volume than the leaves and large amounts of water are held externally by dense tomenta. While both forms have exceptionally high ratios, that of the tomentose form is six times higher. The same difference in ratios is shown by the two forms of *Schistidium antarcticum* although the values are about 20 times less. The cushion form has a wide range of dry weights and moisture contents, the former being augmented by the incorporation of fine soil particles into the almost spherical entire growths. In the

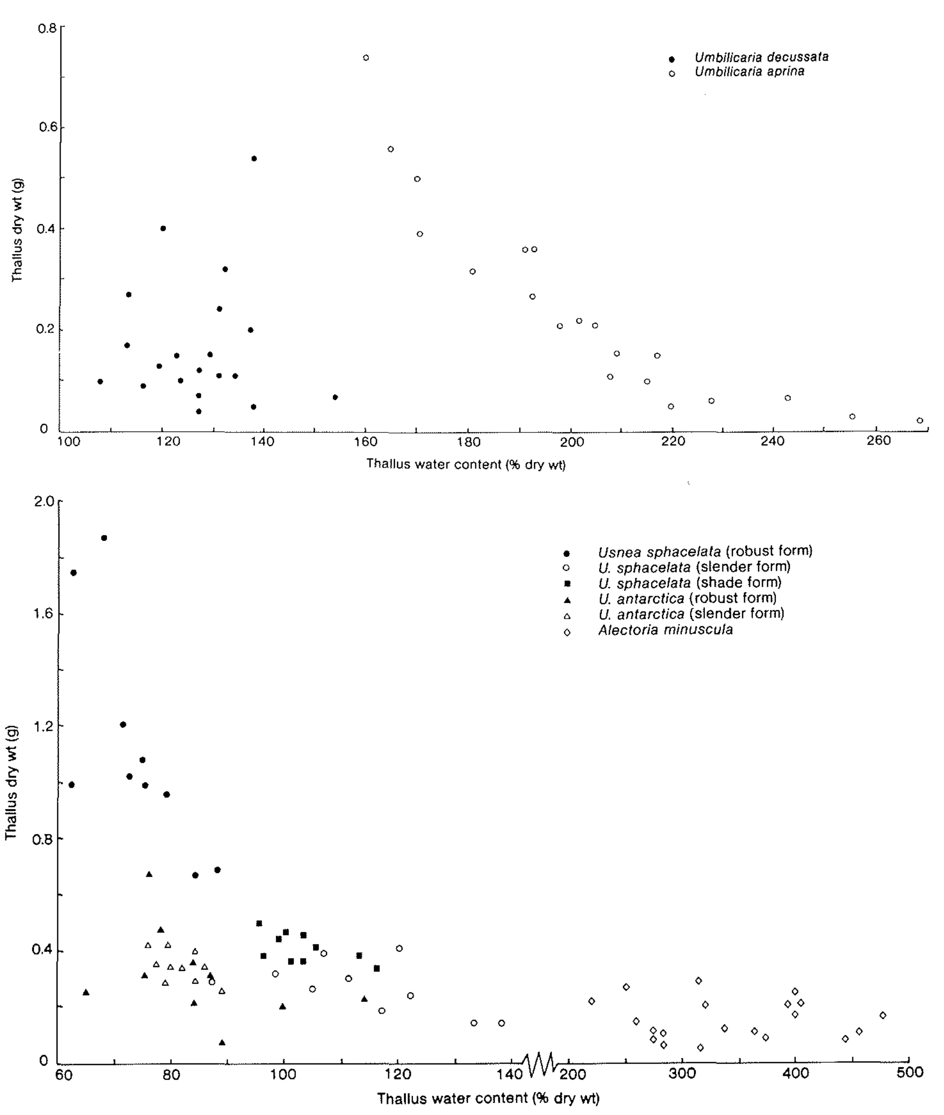

Fig. 9b: Relationship between maximum water holding capacity (as percentage dry weight) and sample dry weight in lichen thalli.

turf form, cut to comparable size and exhibiting much less diversity in colony weight, there is a much closer correlation between water content and weight, although the range of water content is much greater.

The fruticose lichens exhibit a distinct trend which is clearly related to the morphological characteristics of the thallus, the ratios increasing with increasing fineness and density of the branches. Thus, in the robust form of *Usnea sphacelata* (in which the dry weight is very variable, but not so the water content) there is a low ratio, whereas in the fine form of the same species (in which dry weight is relatively constant but water content is variable) the ratio is six times higher; in the shade form both parameters are less variable and the ratio is intermediate. In *U. antarctica*, although the robust form has a wide range of water contents and dry weights compared with those of the slender form, the ratios of the mean values are similar. However, the filamentous mats of *Alectoria minuscula* exhibit a remarkably high span of water contents in thalli of low and similar weight, giving rise to an exceedingly high ratio.

Species and growth form	No. of samples	Ratio	r
Bryum algens			
(sparse rhizoids)	15	2991	0.683
(dense rhizoids)	15	14416	−0.908
Schistidium antarcticum			
(cushion form)	10	101	−0.430
(turf form)	10	631	−0.755
Usnea sphacelata			
(robust form)	10	67	−0.720
(slender form)	10	438	−0.550
(shade form)	10	252	−0.600
Usnea antarctica			
(robust form)	10	275	−0.400
(slender form)	10	244	−0.598
Alectoria minuscula	20	2270	−0.049
Umbilicaria decussata	20	746	−0.047
Umbilicaria aprina	20	853	−0.887

Tab. 4: Maximum water holding capacitys to dry weight ratios and correlation coefficients (r) for lichen thalli and moss colony samples.

There is a marked difference in behaviour between the two Umiblicarias. There is little correlation between thallus weight and maximum water content in *U. decussata* which has no rhizines on its lower surface and has a strongly convoluted upper surface. However, in *U. aprina*, which has dense rhizines but a plane upper cortex, there is a strong negative correlation between thallus weight and water holding capacity. This is similar to the situation with the tomentose *Bryum algens*. The larger plants have a lower density of rhizines and consequently hold considerably less water than the small thalli which have much denser rhizines, but both species have similar high ratios.

5. DISCUSSION

This study has indicated that there are major differences in the water holding capacity of individual species of moss and lichen, and that this is largely dependent on growth-form. Even within a species there can be large differences in water content at full hydration, resulting from certain specialised features (which may be considered as adaptations to inhibit water loss or enhance water uptake). These features appear to be essentially allogenic in nature and develop in accordance with the prevailing environmental conditions experienced by a species, rather than by preadapted forms of that species occupying selected habitats.

There does appear to be some degree of correlation between the water relations characteristics of individual species and their micro-distribution in situ (see SMITH 1988, in press b). Thus, those mosses occupying the wettest sites also have the greatest capacity to store water both externally and internally, while on dry windswept substrata the same species are capable of holding only a small amount of water. Lichens growing in situations where free water is frequently available can maintain high tissue and, in prostrate growth forms external, water contens, while those in progressively drier and more exposed habitats have considerably lower water holding capacities.

Although few comparative studies have been made of sequential water loss in a desiccating atmosphere or of water vapour uptake in a humid atmosphere, the results obtained here correlate well with those of other workers investigating closely related species. Thus RIED (1960) found that *Umbilicaria polyphylla* and *U. erosa* (morphologically similar to *U. decussata* and *U. aprina*, respectively) achieved minimum thallus water contents (*c*. 15% of the maximum) after only about 6—8 hours at 60% relative humidity. When exposed to desiccating conditions LARSON (1979) showed that in *U. vellea* (rhizinate, with plane pruinose upper cortex, cf. *U. aprina*) there is a definite relationship between surface area to dry weight ratio and size, with small, presumably younger, thalli having much greater surface area: weight ratios than in older larger plants. No such dependence was found for the erhizinate *U. papulosa* which has a rugose upper cortex (cf. *U. decussata*). The high water contents of the filamentous thallus of *Alectoria minuscula* supported LARSON's (1979) finding that *Bryoria (= Alectoria) nitidula* has an exceptionally high ratio of surface area to mass, which accounts for its high water holding capacity; the more finely and densely branched compact thalli of *A. minuscula* would be responsible for the higher water content (*c*. 350% compared with *c*. 200% in *B. nitidula*). GIMINGHAM & SMITH (1971) showed that individual shoots of maritime Antarctic mosses lose water very much faster than colony samples in a relative humidity of

45% and that resistance to water loss depends on the area of exposed evaporative surface in relation to the volume of the shoot, changes in the evaporative surface due to changes in leaf configuration as dehydration proceeds, and to increased internal resistances to the movement of water towards the surface.

The few studies previously made on water vapour uptake by Antarctic lichens provided maximum water contents remarkably similar to those obtained in the present experiments, i. e. reaching between 55 and 95% dry weight in *Usnea aurantiaco-atra* (= *U. fasciata*) and *Himantormia lugubris* (KAPPEN 1985a, b), *Usnea sphacelata* (= *U. sulphurea*) and *Umbilicaria decussata* (KAPPEN 1985c), and *Usnea aurantiaco-atra* and *Umbilicaria antarctica* (LANGE & KILIAN 1985). Other fruticose and foliose species, including *Psuedephebe* (= *Alectoria*) *minuscula*, were in the same range, although those with cyanobacteria phycobionts, the frutico-crustose *Caloplaca regalis*, and species of *Umbilicaria* with very thin thalli, had lower water contents (LANGE & KILIAN 1985). Maximum water uptake by Antarctic mosses was usually achieved after *c*. 24—48 hours exposure in a saturated atmosphere (GIMINGHAM & SMITH 1971), complementing the findings in the present experiments. The range of water contents attained by short cushion and turf growth forms was similar in both studies (*c*. 50—80% dry weight).

When exposed to a stream of mist, rhizinate *Umbilicaria vellea* and *U. mamillata* reached maximum thallus water contents of *c*. 175% dry weight (after about 40 min) and 275% (10 min), respectively, but substantially less in samples from which rhizines had been removed (LARSON 1981). However, a considerable reduction in water uptake was demonstrated when the lower cortex was treated with water repellent, whereas similar treatment of the upper cortex had little effect on water uptake. This clearly illustrated the importance of rhizines and the lower cortex in general in facilitating absorption and storage of water. Cushions of *Grimmia* = *Schistidium apocarpa* (similar to, but larger-leafed than *Schistidium antarcticum*) took considerably longer (2 hours) to reach saturation (*c*. 250% dry weight).

In the relatively extreme conditions of coastal continental Antarctica, substrate and atmosphere moisture and temperature regimes are seldom constant for long periods. Consequently, survival of the avascular cryptogamic flora depends on the ability of species to tolerate considerable fluctuations in tissue water content ranging from full hydration or even flooding to extreme desiccation, often within an hour or two. This is demonstrated in Table 5 in which the water content in three macrolichen species is compared in situ during a cold sunny afternoon with low relative humidity, and several hours later when the plants were lightly covered by snow which quickly melted. Thalli of both *Alectoria* and *Umbilicaria* exhibited rapid contraction when dry and expansion when wet. During desiccation events both may reduce in surface area by about 50% (Fig. 10). Conservation of water is primarily a function of the hydration state at the onset of a desiccation event. Such hydration/dehydration cycles coupled with either high or low tissue temperatures must impose severe physiological stress on those plants in which tissue water contents adequate for optimal photosynthesis, and hence net production, often occur for only brief periods in any one day or sequence of days during the growing season.

Weather conditions on 25 November 1985	*Usnea sphacelata*	*Alectoria minuscula*	*Umbilicaria decussata*
1500 hr Air temp at 5 cm: 2° C R.H. at 5 cm: 45% Sunshine for 7 hr	8.6 ± 0.2	10.5 ± 0.3	12.1 ± 0.5
1900 hr* Air temp at 5 cm: 0.5° C R.H. at 5 cm: 96% Cloudy with snow for 1 hr	104 ± 6	336 ± 14	142 ± 5

Tab. 5: Field thallus water contents (%dry wt.) in three macrolichen species during desiccating and saturating events. * After lightly blotting to remove superficial water. Data are means of 20 plants ± one standard error.

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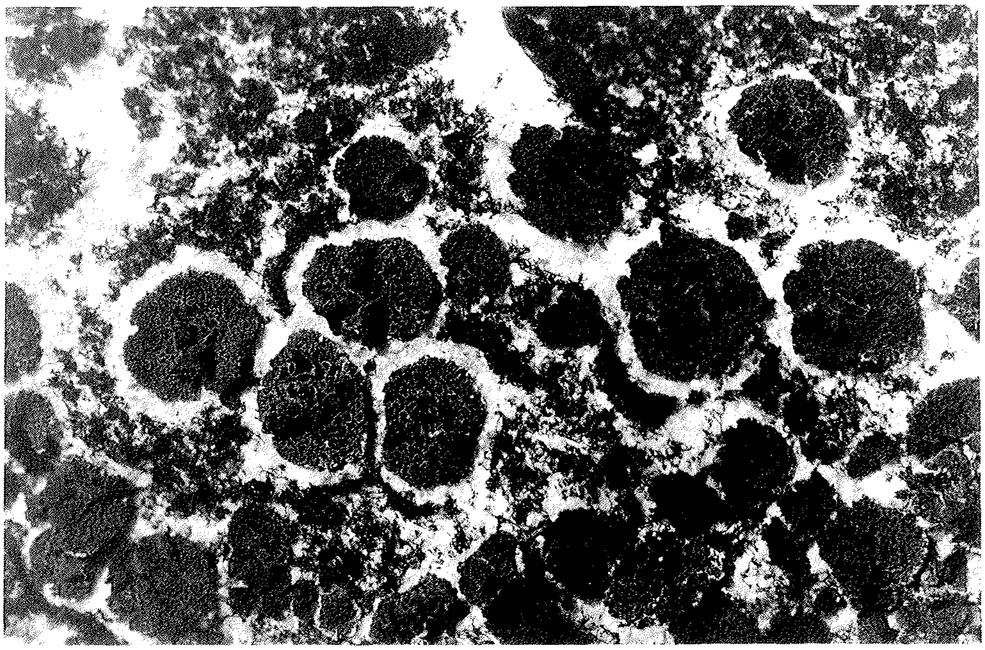

Fig. 10: Thalli of *Umbilicaria decussata* in situ in dry state. Filamentous colonies of *Alectoria minuscula* occur between the *Umbilicaria* thalli. Note the uncolonised rings of bare rock around each thallus indicating the extent to which they expand when fully haydrated.

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